Final Report
February 28, 1975

THE MEDICINE BOW ECOLOGY PROJECT

Prepared for the

Office of Atmospheric Water Resources
U.S. Bureau of Reclamation
Department of the Interior
Denver, Colorado 80225

by

The University of Wyoming
Laramie, Wyoming 82071

in cooperation with

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EXPERIMENT STATION

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16. ABSTRACT

In addition to baseline data, the Report includes 1) the results of studies on the impact of snow on herbaceous and shrubby vegetation, elk, deer, trout, lake phytoplankton, and litter decomposition; and 2) the movement of Ag in an alpine ecosystem, the natural concentration of Ag at 20 locations in the Mountains, and the toxicity of Ag to tufted hairgrass, lodgepole pine seedlings, and rainbow trout. Ecological changes resulting from cloud seeding probably will be very slow, assuming that annual snowfall will be increased by only about 15 percent and only above about 2700 m elevation, and that snow cover duration will be prolonged by only a few days, if at all. The general discussion emphasizes the need for accurate information on the amount, distribution, and duration of the additional snow produced by cloud seeding in order to accurately evaluate impact; the fact that cloud seeding will be but one of several human influences on the ecosystems; and that there is the potential for indirect, undesirable impacts on areas downstream from where the seeding occurs. Six recommendations are listed that seem desirable from an ecological perspective, and information gaps are identified.

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FINAL REPORT

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The Potential Sensitivity of Various Ecosystem Components to Winter Precipitation Management in The Medicine Bow Mountains, Wyoming

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INTRODUCTION AND OBJECTIVES

Dennis H. Knight

Regardless of the specific resource being managed, the management techniques always lead to secondary ecological changes. This occurs because of the many interactions that are characteristic of the ecosystems in which man operates. The ecological changes that occur may not be detrimental, but sometimes they are and any modern management program should have sufficient ecological information so that unfortunate consequences can be avoided or minimized.

Precipitation management is a rather new way of modifying ecosystems, and consequently little is known about the potential secondary changes that may occur where rainfall or snowfall is increased over a period of years. With this in mind, and in anticipation of a winter cloud seeding program for the Medicine Bow Mountains of Wyoming, an interdisciplinary research program was initiated to 1) predict probable secondary effects, if any, of the planned winter cloud seeding program, and 2) provide a basis for evaluating the ecological impact of cloud seeding when it actually occurs. The basic question for the Medicine Bow Project was, "How will the ecosystem change if the mean annual snowfall is increased by cloud seeding with silver iodide?" Since it has been financially impossible to develop a research program to study the entire ecosystem, our research focused on the sensitivity of certain key components and processes in the ecosystems of the Medicine Bow Mountains. In addition to baseline data, this final report includes the results of seven separate studies:

1. The impact of snow on elk.
2. The impact of snow on mule deer.
3. The impact of snow on herbaceous and shrubby vegetation.
4. The impact of snow on litter decomposition and nutrient leaching.
5. The relationship between trout ecology and annual snowpack.
6. The effect of spring run-off on subalpine lake phytoplankton.

7. The movement and ecological effect of silver iodide.

Each of the above sub-projects is reported on separately, but the Discussion Section (p. 365) includes an attempt to integrate the results whenever it seems reasonable and logical to do so.

The contract between the Bureau of Reclamation and the University of Wyoming was established in September, 1971, and shortly thereafter a Cooperative Agreement (No. 16-252-CA) was established between the University and the Rocky Mountain Forest and Range Experiment Station (U. S. Forest Service). Nearly all of the Medicine Bow Mountains lie within the Medicine Bow National Forest, and Forest Service scientists (Thilenius and Ward) worked closely with University scientists in developing the research program. Numerous meetings were held during the winter of 1971-72 in order to select study areas and evaluate research design. Considerable effort was devoted during this time to the synthesis of existing knowledge about the ecosystems of the Medicine Bow Mountains.

Field work began as soon as possible in 1972, and continued until late summer, 1974. Most of the data were gathered in the spring and summer, but some field work was done during the winter as well. Several projects were scaled down or eliminated in early 1973 due to an unexpected budgetary restriction, however a subsequent addition to our budget in late 1973 and a new agreement (Amendatory Agreement No. 1) with the Bureau led to a 7 month extension. We have been able to accomplish the principal objectives of our original proposal, though some questions remain unanswered about the ecological effects of cloud seeding with silver iodide. We identify these unanswered questions along with our results.

General Research Design

At least four approaches can be utilized for evaluating the ecological impact of weather modification:

1. controlled large-scale experiment approach.
2. controlled small-scale experiment approach.
3. before-and-after monitoring approach.
4. systems analysis approach.

The discussion that follows describes briefly a rationale that has been useful for determining the best approach for each of the seven studies that are part of the Medicine Bow Ecology Project.

Controlled large-scale experiment approach

An ideal option would seem to be the location of two very comparable watersheds, one of which would be seeded to increase snowfall and the other not seeded. After considerable discussion, this approach was essentially abandoned for the following reasons. First, it seemed doubtful that a legitimate control of watershed size could be found. Two areas of several square kilometers would most likely be too different in microclimate and vegetative cover, so that differences that occurred after the treatment probably could not be attributed confidently to the snow-treatment effect. Secondly, because the treatment effect could possibly be difficult to detect in a short time, several field seasons would probably be required just to select the two "comparable" watersheds. Careful measurements would be required from a large number of watersheds before the best combination could be selected. Thirdly, the best two watersheds for such an experiment would probably be adjacent, and there is the question of whether a cloud seeding operation could prevent artificial precipitation on the control. Because of these problems, the Medicine Bow Project has focused more on small-scale experiments, where controls can be more easily established.

Controlled small-scale experiment approach

The advantage of this approach is that controls are more easily established and replications are possible. The snow treatment or

silver iodide treatment, of course, must be applied in some manner other than seeding, but meaningful data can be obtained for some organisms, in particular small plants and micro-organisms. Analysis of variance can be used to evaluate treatment effect with a certain degree of confidence. This approach was used in the Medicine Bow Project for one vegetation study and two studies on silver iodide toxicity.

Before-and-after monitoring approach

This approach is desirable because no control is necessary and actual cloud seeding provides the snow treatment. It is a desirable phase of any impact study and has been an important approach for the Medicine Bow Project. Considerable baseline information is included in this report.

The disadvantages with the before-and-after approach are that the impact is not known until it's happened over a large area, which seems like a poor management approach, and there is often the question about whether the changes that occurred after the cloud seeding were in fact caused by the seeding or some other natural phenomenon. We can expect this problem in the case of winter precipitation management because the secondary ecological effects are not likely to be observed for several years, if not decades. The ecosystems are already adapted to considerable year to year fluctuations in snowfall, so changes will probably result from a modified mean annual snowfall or a modified sequence of heavy and light snowfall years. The accumulation of Ag compounds to toxic levels is also likely to be slow.

The system analysis approach

Invariably an evaluation of impact calls for an analysis of the ecosystems in which a new management program is planned. These ecosystems are sufficiently complex that rarely is a total system analysis possible. Experience gained from the International Biological Program suggests that such an effort is also expensive. However, to one degree or another, using various tools and with variable success, ecologists for years have worked toward gaining a better understanding of ecosystem structure and function. Usually the focus has been on sub-systems for

pragmatic reasons. With the development of computer simulation techniques a new tool has been gained for learning about ecosystems, one that has the potential of allowing a total system analysis of natural and man-dominated ecosystems.

The short duration and funding level of the Medicine Bow Ecology Project have not permitted a total system analysis for the Medicine Bow ecosystem. We have used whatever tools seemed appropriate, however, to gain an understanding sufficient to predict the ecological effect, if any, of winter cloud seeding with silver iodide on certain components and processes (sub-systems) in the Medicine Bow Mountains. This research approach involved the synthesis of data that we and others have collected on various ecological relationships in the Medicine Bow Mountains, e.g. the relationship between natural snow depth and elk migration or plant distribution. In some cases this approach has led to the identification of limiting factors. If it can be confidently predicted that cloud seeding will modify a limiting factor, then we can confidently predict that the distribution or abundance of the organism to which the factor is limiting will be modified. To predict the degree of modification quantitatively is rarely possible, however, without a total system analysis.

Another value of systems analysis is that it forces attention to the unknown. In this report we list the additional questions that remain unanswered and which seem particularly germane to evaluating the ecological impact of winter precipitation management.

THE MEDICINE BOW MOUNTAINS: A BASELINE DESCRIPTION

The ecological changes that may occur following winter cloud seeding are likely to be slow and subtle, especially since there is already considerable yearly fluctuation in snowfall and there will probably be no seeding during the heavy snowfall years. It seems reasonable to expect that any changes that do occur will be the result of 1) less variability in snowfall from year to year, a potentially important ecosystem characteristic; 2) an increase in the mean annual

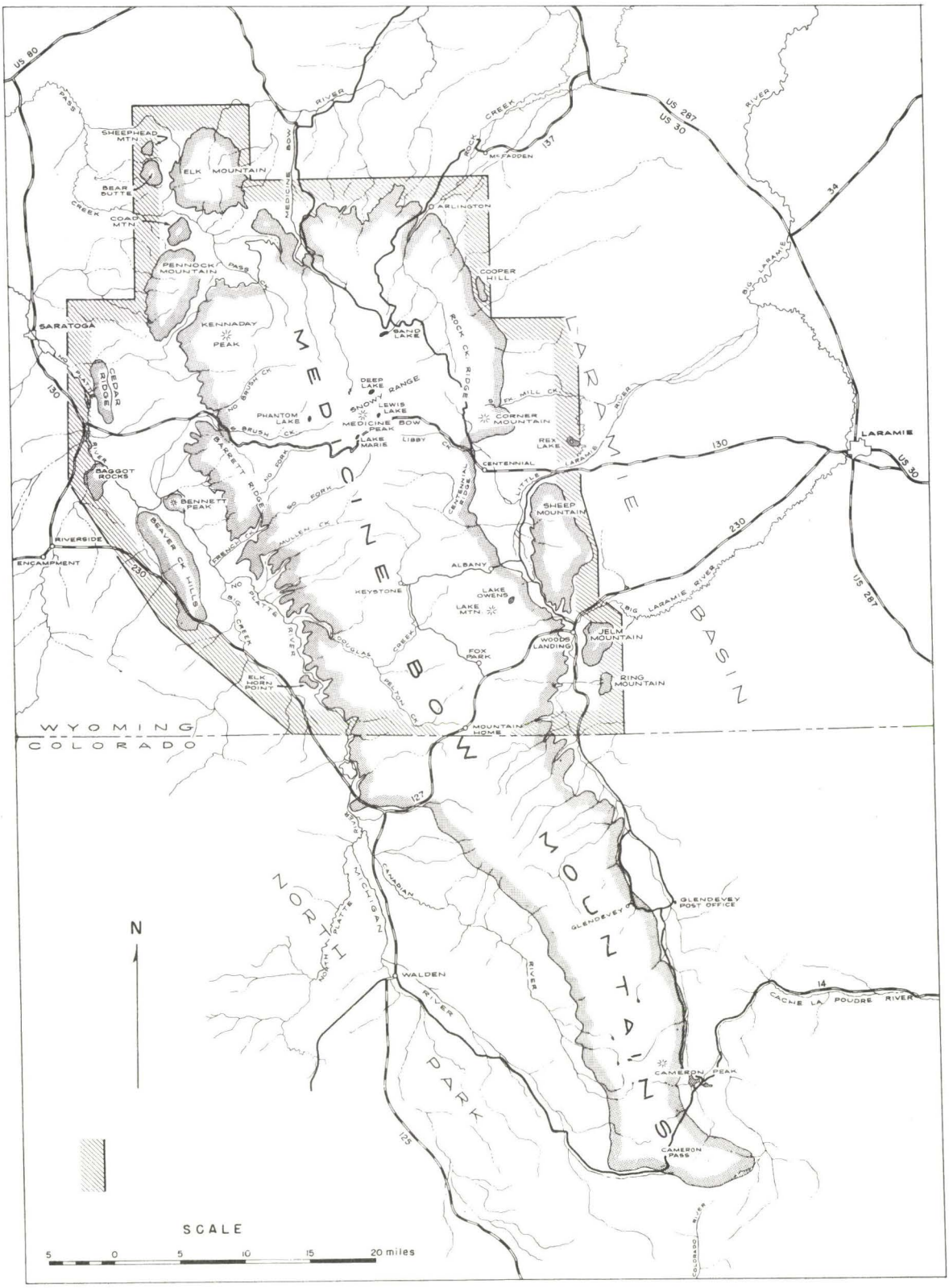

Fig. 1. Map of the Medicine Bow Mountains (from Houston et al. 1968).

snowfall; or/and 3) an increase in the amount of potentially toxic silver or iodide compounds in the environment. Such changes are difficult to predict during a short-term research program, though much of our work was designed for that task, and they may not occur until after 10 or more years. At that time, however, there may be questions about what the ecosystems of the Medicine Bow Mountains were like prior to the initiation of cloud seeding. We do not have every useful bit of baseline information, but during the course of our research a considerable amount of information has been synthesized.

GEOLOGY AND SOILS

The Medicine Bow Mountains[1] are located in southeastern Wyoming, 48 km west of Laramie, and are composed primarily of a complex uplifted mass of Precambrian rock (Houston, et al. 1968). Sedimentary rocks of Paleozoic, Mesozoic, and Tertiary age are found in the center of the range as well as on the flanks. Pleistocene glacial deposits are abundant in the north, having originated from an ice cap near Medicine Bow Peak (3,640 m elevation). Surrounded by plains that are about 1,800 to 2,100 m in elevation, the mountains rise rather abruptly to a rolling plateau at about 3,180 m. Libby Flats comprises much of this plateau which is broken by the Snowy Range, a 10-km long axial remnant in the north-central portion of the mountains. The Rawah Range is an axial remnant in the Colorado portion of the Medicine Bow Mountains. Since cloud seeding would probably be effective only above about 2,700 m, the usual bottom of the orographic clouds on the western slopes, it is of interest to note that about 49 percent of the Medicine Bow Mountains are above 2,700 m in Wyoming (approximately 677 km^2).

The soils of the Medicine Bow Mountains have not been studied extensively, and most of the literature on mountain soils focuses on

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[1] The Medicine Bow Mountains extend south into Colorado, but this report is limited primarily to the Wyoming portion, Fig. 1.

the alpine area. Nimlos and Pattie (1965) suggest that alpine soils are those with a mean annual temperature less than 1.6°C and a mean summer soil temperature less than 4.4°C.

Chemical, mineralogical, and morphological data all indicate that the development of alpine soils is limited. Slow development of alpine soils and cold temperatures also affect the numbers of soil microorganisms. Rall (1965) isolated 32 species of soil fungi on Libby Flats in the Medicine Bow Mountains. It was interesting to note that neither the number of species nor total number of organisms decreased with increasing depth of sampling. Rall's data suggest that soil fungal populations in cold areas are much lower than in temperate and tropical areas.

Johnson and Billings (1962) found most alpine mineral soils on the Beartooth Plateau in Wyoming have the textural composition of a gravelly, sandy loam. The gravel content varies somewhat but usually increases with depth. Clay content is conspicuously low in alpine soils. Johnson and Billings (1962) report clay amounts ranged from 0.5% in a frost boil to 12% in an alpine bog soil.

Smith (1966) tested the nutrient status of two subalpine meadow soils in the Medicine Bow Mountains. The two soils responded similarly to the addition of nutrients. Nitrogen, potassium, and micronutrients resulted in no increase in the yield of shoots, roots or shoots plus roots. The addition of phosphorous, however, resulted in about a 100% increase in root yield and 60% increase in shoot yield, which suggests that phosphorus is a limiting factor.

Thilenius (this study) studied the soils on Libby Flats and on the west slope of Medicine Bow Peak (see p. 24 for locations). He found considerable pedogenic development at both sites, with the sola (A and B horizons together) ranging from 6 to 38 cm deep. The sola at the Libby Flats site was medium-textured with up to 40% stones, while the other site had finer textured and generally stone-free sola. Both soils were well-drained, though short-term saturation was obvious on Libby Flats in the spring. On Libby Flats the boundary between dark upper horizons and the light subsurface horizon was abrupt.

The pH at both sites was about 4.4 at 0-4 cm depth, 3.9 at 4-20 cm, and 4.0 at 20-50 cm.

Oosting and Reed (1952) studied spruce-fir forests in the Medicine Bow Mountains and found without exception that there were boulders of varying sizes exposed in every stand, some igneous and some metamorphic in nature. The litter layer was always thin, 3 to 13 mm, and the soil profiles varied little from stand to stand. Somers (1951) observed podzolization in all the spruce-fir stands he studied, especially on the ridges where the most mature soils were found. He found that most of the roots were in the B horizon, and that the A horizon had a mean pH of 4.7 and about 45% sand, 24% clay, and 31% silt. Somers (1951) observed that spruce seemed most common on the more silty and clayey soils. By contrast Jacoby (1971) and Severson (1963) found aspen most frequently on sandy loam to loamy soils.

Moir (1969), working in Colorado, found that well-drained soils derived from coarse-textured granites or granodiorites were frequently covered with lodgepole pine forest, a common forest type in the Medicine Bow Mountains. Surface mineral horizons were generally found to be gravelly loamy sands or gravelly sandy loams and in some stands were considered cobbly. Surface humus horizons were found to form a nearly continuous mat about 2 to 3 cm thick, somewhat thicker than the spruce-fir litter. Reynolds & Knight (1973) found no significant difference in the litter depth of lodgepole pine forest and spruce-fir forest in the Nash Fork Watershed, Medicine Bow Mountains.

NATURAL SILVER CONCENTRATIONS IN THE MEDICINE BOW MOUNTAINS

Paul Singleton and Randall White

The natural silver concentrations in soil, foliage, and litter were studied in 1972 and 1973. The objective of this effort was to determine natural concentrations of potentially toxic Ag in the environment, so that at some future time it would be possible to determine if cloud seeding with AgI had resulted in a significant increase of Ag.

Twenty sites were located to give a fairly even geographic representation of the proposed target area (Fig. 2). With one exception (site 20), the sites were chosen where communities of aspen, lodgepole pine, Engelmann spruce, and grass vegetation could be found in close proximity. Each site was sampled at 3 different times -- spring and fall 1972 and spring 1973.

Samples of soil, foliage, and litter were collected from all tree communities, and soil and foliage were collected from grass communities. Five trees from each forest community at each site were selected for sampling. Foliage collected from the five trees was combined into a composite sample to represent that community at that site. Soil and litter were also collected from under the same five trees and combined into composite soil and composite litter samples. Foliage and soil were collected from a circular area of four meters in diameter at each grass community. Plastic gloves were worn to prevent contamination.

Tree foliage was sampled by breaking small branches from the five trees at each site. Grass vegetation was pulled from the plant in preference to clipping to eliminate the possibility of contamination by clippers. Litter was sampled from under the appropriate tree species by simply collecting the litter in a manner which gave a representative sample from under each of five trees of each species at

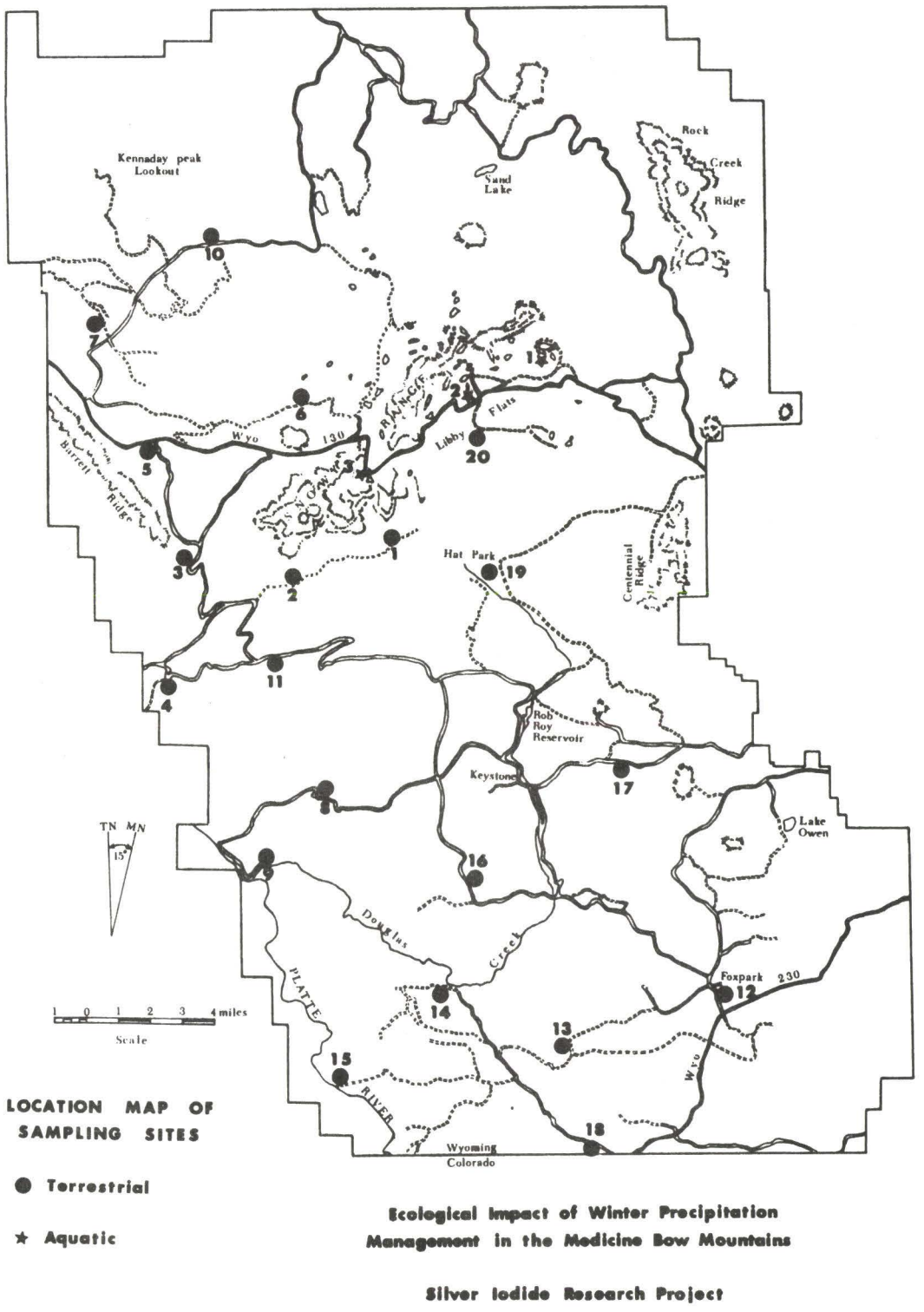

Fig. 2. Map showing the location of all samples used to determine natural silver concentration.

each site. Soil was sampled by scraping litter from the surface and with a shovel removing the top 2-3 cm of soil. Care was taken so soil touched by the shovel was not included.

The samples were submitted to a commercial laboratory for silver analysis. The laboratory used the pyrosulfate fusion method for silver determination which involves drying, pulverizing and ashing the sample, fusion with potassium pyrosulfate, solution with nitric acid, extraction with TOTPMIBK organic solvents (tersooctyl phosphorthioate-methyl isobutyl ketone), and determination of silver by atomic absorption. The detection limit for this method is .008 ppm Ag in ash.

Results[1]

Table 1 summarizes the Ag concentration data. Soil under lodgepole pine contained significantly less Ag than soil under spruce, aspen, and grass, while lodgepole foliage contained significantly greater Ag than the foliage of the other three species. It is evident that lodgepole pine accumulates greater amounts of Ag than the other three species. Spruce, on the other hand, has a tendency to accumulate less Ag than the other species, although not significantly less. Spruce litter, however, contained significantly less Ag than lodgepole and aspen litter.

TABLE 1. Mean values for silver concentration in each component sampled on the three sampling dates, expressed as ppm.

	Soil	Foliage	Litter	n
Lodgepole	0.032 a	0.016 a	0.030 a	57
Spruce	0.053 b	0.006 b	0.006 b	60
Aspen	0.048 b	0.010 b	0.026 a	57
Grass	0.055 b	0.008 b	--	60

Values with different letters in each column are significantly different at .05 level.

[1] A detailed description of the results can be found in White (1973).

Mean values were calculated for each sampling site to determine if geographic location had an influence on the content of silver in soil and foliage. Spruce, aspen, lodgepole, and grass values were combined at each site for each of the sampling dates. Figure 3 is a map of the study area showing the average ppm Ag in foliage at each site. As is evident there are areas of high and low concentrations of silver in the soil. The area delineated as high contains ten sampling sites with soil silver ranging from .208 ppm to .042 ppm (soil mean = 0.82, foliage mean = 0.11). The ten sites located in the area delineated low contained from .037 to .009 ppm silver in the soil with a mean of .021 ppm. The mean content of Ag in the foliage in the low area was .009, only slightly less than the .011 ppm mean for the high area.

The plants growing at lower elevations, although having less Ag in the soil to draw from, accumulate almost as much Ag as the plants growing at higher elevations. It is possible the warmer temperatures and better growing conditions cause growth to be more rapid at lower elevations and thus almost as much silver could be transported into plants at lower elevations, even though more silver is present in the soil at higher elevations. The higher silver in the soil at these elevations could be related to the greater abundance of Medicine Bow metaquartzite.

The Ag concentrations observed at the 3 sampling times at each site were compared, in order to determine if seasonal differences existed (White 1973). As might be expected, the soil samples were not significantly different (p 0.05). Lodgepole pine and aspen foliage were also not significantly different between the 3 sampling dates, but it is interesting that in lodgepole there was a trend toward higher concentrations of silver in the fall while in aspen this trend was reversed, with more silver in the spring samples. Grass, like aspen, shows a marked spurt of growth in the spring and the results are similar. The content of Ag in grass foliage was .008 ppm in the spring 1972 and .013 ppm in the spring of 1973, both values being significantly greater than the 1972 fall value, .004 ppm.

The Ag content of aspen litter was significantly higher in the spring (.033 ppm in 1972 and .036 ppm in 1973) than in the fall of 1972 (.019 ppm). No trend was apparent for spruce and pine litter. The pine and aspen litter contain approximately the same amounts of Ag while spruce litter contains less.

The Ag content of the foliage and underlying soils of grass, spruce, lodgepole pine, and aspen were compared (White 1973). Regression techniques suggested that an increase in soil Ag will result in grass and aspen accumulating more Ag than spruce and pine, but the difference is very slight. A one unit increase in soil Ag concentration results in a 0.03 unit increase in aspen and grass foliage Ag and a 0.02 unit increase in spruce and pine foliage Ag.

Less variation in the Ag data is evident in the fall than in the spring, suggesting that fall is the best time to sample for Ag concentration in the future.

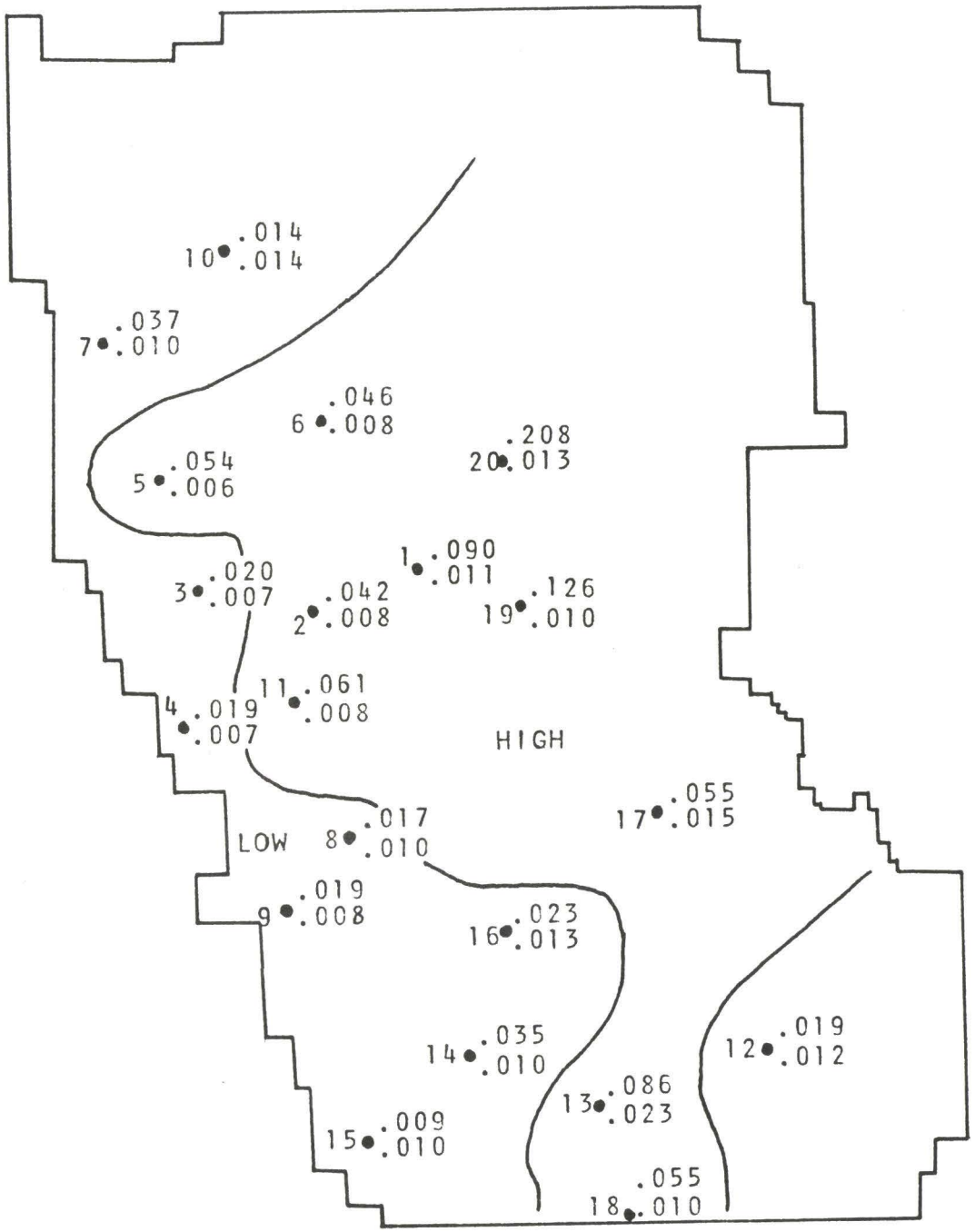

Fig. 3. Map showing Ag concentrations in soil (top number) and foliage (bottom number). The data for foliage concentration are averages for aspen, spruce, pine, and grass samples. For sites 1 - 19, n = 12; for site 20, n = 6.

CLIMATE AND HYDROLOGY

Dennis H. Knight

Previous to the establishment of the Wyoming Water Resources Research Institute (WRRI) in 1965, few measurements of climatic characteristics had been made in the Medicine Bow Mountains proper. Since that time, however, a network of meteorological stations has been established and recently the data have been summarized (Rechard & Smith 1972). Snowpack and streamflow data are available from the Soil Conservation Service, the U. S. Geological Survey, and WRRI[1]; and we have gathered summer data on solar radiation, temperature, relative humidity, and precipitation. Though data are still not sufficiently accurate to prepare isoline maps, the range of climatic conditions can be described in a general quantitative manner.

As can be expected in mountains ranging from 2,134 to 3,658 m elevation at about 41.4° latitude north, temperature fluctuations are great, both seasonally and diurnally. At Foxpark (2,760 m) the mean January temperature is -10°C, while in July the mean is +11°C (U.S.D.A. 1941). Though daytime summer temperatures range from 21 to 32°C, frost may occur at night during any summer month at the higher elevations. Along an elevational gradient, the mean annual temperature, measured in standard U. S. Weather Bureau Shelters, ranges from 3.5°C at Centennial (2,574 m) to -2°C at Little Brooklyn Lake (3,170 m) (Rechard & Smith 1972).

Prevailing winds in the Medicine Bow Mountains are westerly in origin and are frequently very strong, in the winter especially. Rechard & Smith (1972) report fall and winter winds of 64 km per hour on Libby Flats (c. 3,261 m) and at Little Brooklyn Lake (3,170 m). Pronounced snow drifting is characteristic, and drift patterns are

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[1] Addresses:
SCS, Snow Survey Supervisor, P. O. Box 2440, Casper, Wyoming 82601
U.S.G.S., District Chief, P. O. Box 2087, Cheyenne, Wyoming 82001
WRRI, P. O. Box 3067, University of Wyoming, Laramie, Wyoming 82071

sometimes reflected by the vegetation.

Solar radiation has been measured at several localities, the best year-round measurements being available from WRRI's Little Brooklyn Lake station. As can be seen in Fig. 4, mean daily radiation there ranges from 118 ly/day in December to 483 ly/day in July (4-year averages, 1967-1971).

The mountains receive a large amount of snow during the winter, though the amount may vary over 100 percent from one year to the next. The Soil Conservation Service has data for several snow courses in the Medicine Bow Mountains[1], which show that snow depth on the west slope may vary from 97 to 224 cm (30 to 79 cm water content) at 2,865 m (North Barrett Creek) and 157 to 297 cm (66 to 119 cm water content) at 3,109 m (North French Creek). Snowmelt water is very important to the mountain ecosystems and to the maintenance of stream flow in 8 principle watersheds, all of which contribute water to the Laramie River -- North Platte River drainage (Fig. 1). Over 80 percent of the runoff occurs between April and July, with most streams having 2 or 3 peaks in flow rate due to different melt patterns of high elevation and low elevation snow (Allen and Smith 1972).

Water yield records for the Mountains are maintained by the Supervisor's Office, Medicine Bow National Forest, and are partially summarized in Table 2 and Fig. 5. Generally, the watersheds with a higher average elevation have the highest water yield (acre feet/acre/year), probably a result of greater amounts of snow. Fig. 5 illustrates the variation in streamflow from one year to the next. Other data of this nature are available from the USFS, USGS, and WRRI. Data for Nash Fork Creek are presented in Fig. 40 (p. 248).

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[1] Summary of Snow Survey Measurements, Wyoming. U.S.D.A. Soil Conservation Survey, P. O. Box 2440, Casper, Wyoming 82601.

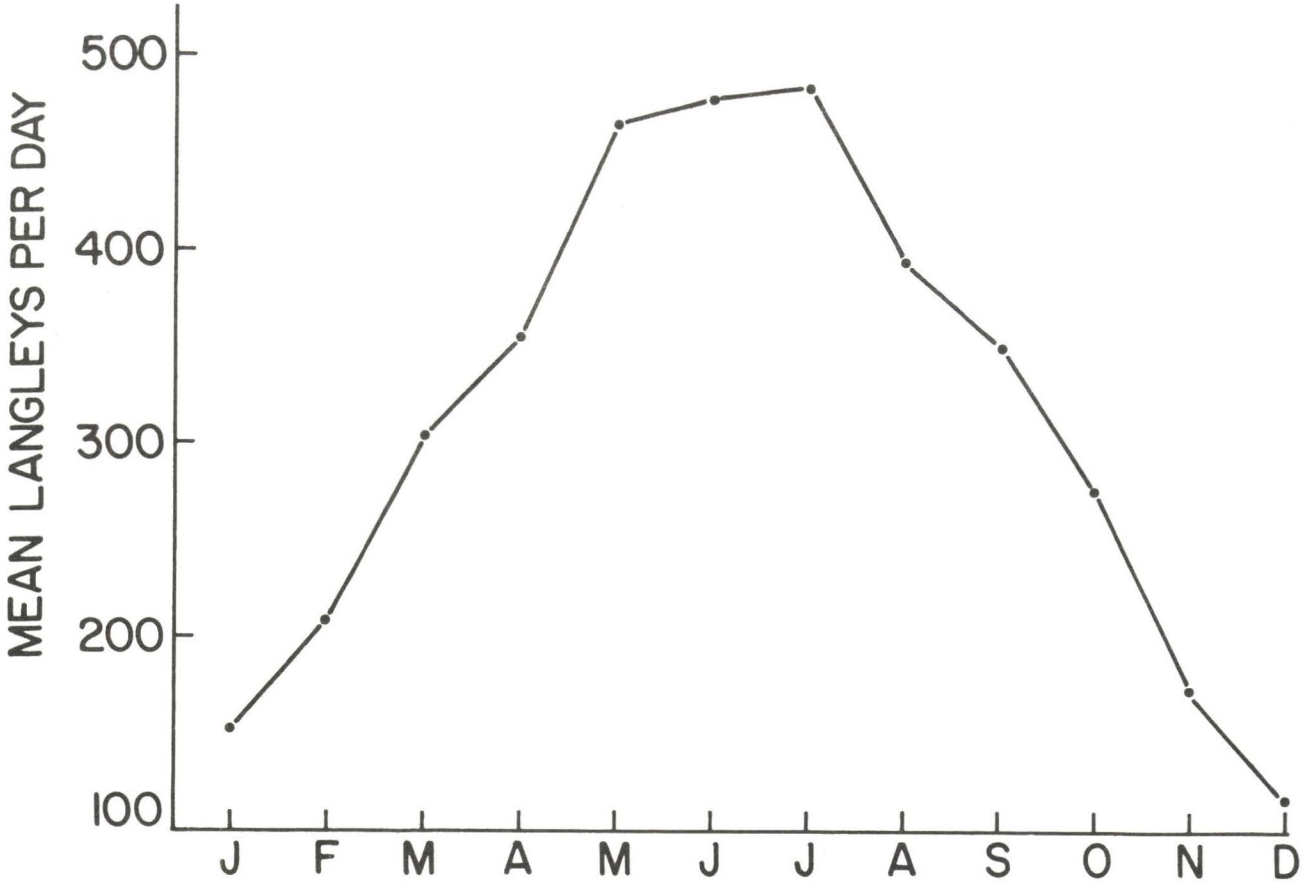

Fig. 4. Average monthly solar radiation at Little Brooklyn Lake, 1967-71, from Rechard and Smith (1972).

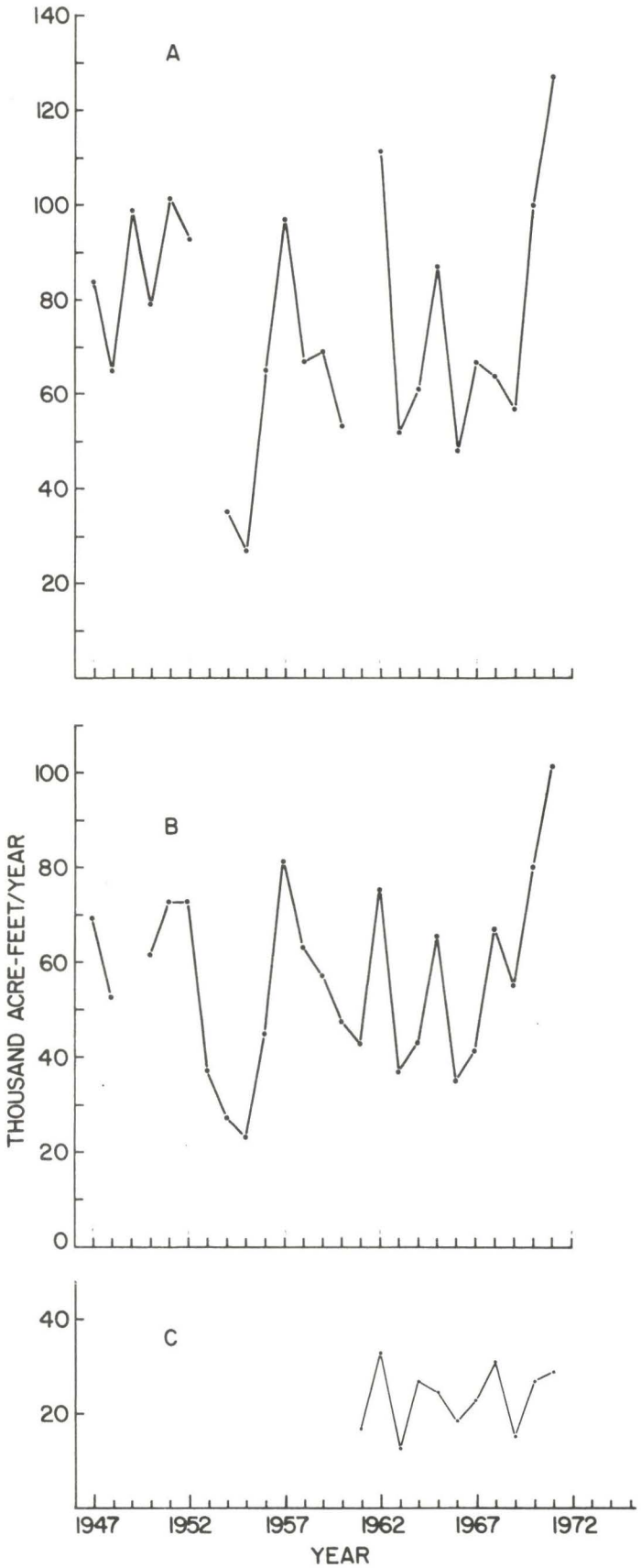

Fig. 5. Annual variation in water yield from the Little Laramie River, Filmore Gauge (A); Douglas Creek below Pelton Creek (B); and South Brush Creek (C). Data from the Supervisor's Office, Medicine Bow National Forest, Laramie, Wyoming.

TABLE 2. Water yield from several watersheds in the Medicine Bow Mountains. Data provided by the Supervisor's Office, Medicine Bow National Forest, Laramie, Wyoming 82070.

	Average Acre Feet/Year	Average Acre Feet/Acre/Year
Little Laramie River	175,634	1.8626
Rock Creek	163,733	1.9149
Douglas Creek	55,166	1.0581
French Creek	98,766	1.5964
Brush Creek	81,599	1.1733
Pass Creek	22,133	0.8421

Very little data on water quality are available for the Medicine Bow Mountains, but the U.S.F.S. has initiated a sampling program in several watersheds to fill this void. Table 3 includes data for the ranges of several streams, and Table 4 contains data specific for French Creek and Brush Creek. The likelihood of increased silver or iodine in the streams as a result of cloud seeding is considered beginning on p. 329.

Most streams have enough coliform bacteria to test unsafe for drinking.

TABLE 3. Ranges for several stream characteristics in the Snowy Range, Medicine Bow Mountains. Source: Supervisor's Office, Medicine Bow National Forest, Laramie 82070.

Parameter	1969	1970
Water Temperature, ^{o}C	3.5-18	8.5-16
Total Hardness, mg/l	20-85	10-46
Dissolved Oxygen, mg/l	7-9	6-7
Turbidity, J.T.U.	0	0
pH	6.7-8.2	6.3-7.5
Alkalinity, mg/l	10-85	10-58
Nitrate Nitrogen, mg/l	0.011-0.042	---
No. Samples	17	9
No. Streams (Snowy Range)	7	9

TABLE 4. Some water quality characteristics for 4 streams on the west slope of the Medicine Bow Mountains. Source: Supervisor's Office, Medicine Bow National Forest, Laramie 82070. a) 6/19/69, b) 8/19/69. For specific sample locations, contact the Supervisor's Office, MBNF, Skyline Road, Laramie, Wyoming 82070.

Stream		Water Temp. °C	Total Hardness ppm	Dissolved Oxygen ppm	Turbidity JTU	pH	Alkalinity mg/l	Nitrate N mg/l
South French Creek	a)	8	50	9	0.0	7.8	50	0.015
	b)	14.5	60	8	0.0	6.7	--	--
North French Creek	a)	7	20	8	0.0	8.2	50	0.028
	b)	11	20	7	0.0	7.0	--	--
South Brush Creek	a)	5	20	8	0.0	7.5	50	0.032
	b)	11.5	20	7	0.0	6.9	--	--
North Brush Creek	a)	5	30	9	0.0	7.4	20	0.035
	b)	11	60	8	0.0	6.9	40	--

Snow Duration and Growing Season Microclimate in Alpine Tundra and Subalpine Meadows

John Thilenius and Dennis Knight

In order to characterize the growing season environment of the Medicine Bow Mountains above 2,700 m, 5 sites (Table 5, Fig. 6) were instrumented as follows:

Air temperature and relative humidity. A continuous record was obtained using a hygrothermograph with the sensing elements at about 20 cm above the ground. The hygrothermograph was enclosed in a small, double-roofed, weather screen (Hungerford 1957). Standard max-min thermometers on a Townsend Support were also mounted in the weather screen.

Precipitation. A 20 cm diameter non-recording rain gauge with the orifice at about 30 cm was located at each site to record growing season precipitation. Rain gauges were read at seven-day intervals during the growing season. Snow duration was observed and depths were gauged at 3 sites using permanently fixed 2 m tall posts (3 m tall at Fourlog Park) marked at 2 dm intervals.

Solar radiation. A recording pyranograph was placed at each site, with the sensing elements about 30 cm high.

In addition 3 of the sites were monitored for wind velocity, using a 3-cup totalizing anemometer at about 50 cm; soil temperature[1], using a 3 pen thermograph with sensors at -5, -20, and -50 cm; and soil moisture, using the gravimetric method biweekly on 25 samples. Unless indicated otherwise, the data were gathered from early June until late August.

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[1] Only one 3 pen thermograph was available in 1972, and it was used on Libby Flats. Two other instruments were installed during 1973 at the Lake Marie and Fourlog Park sites.

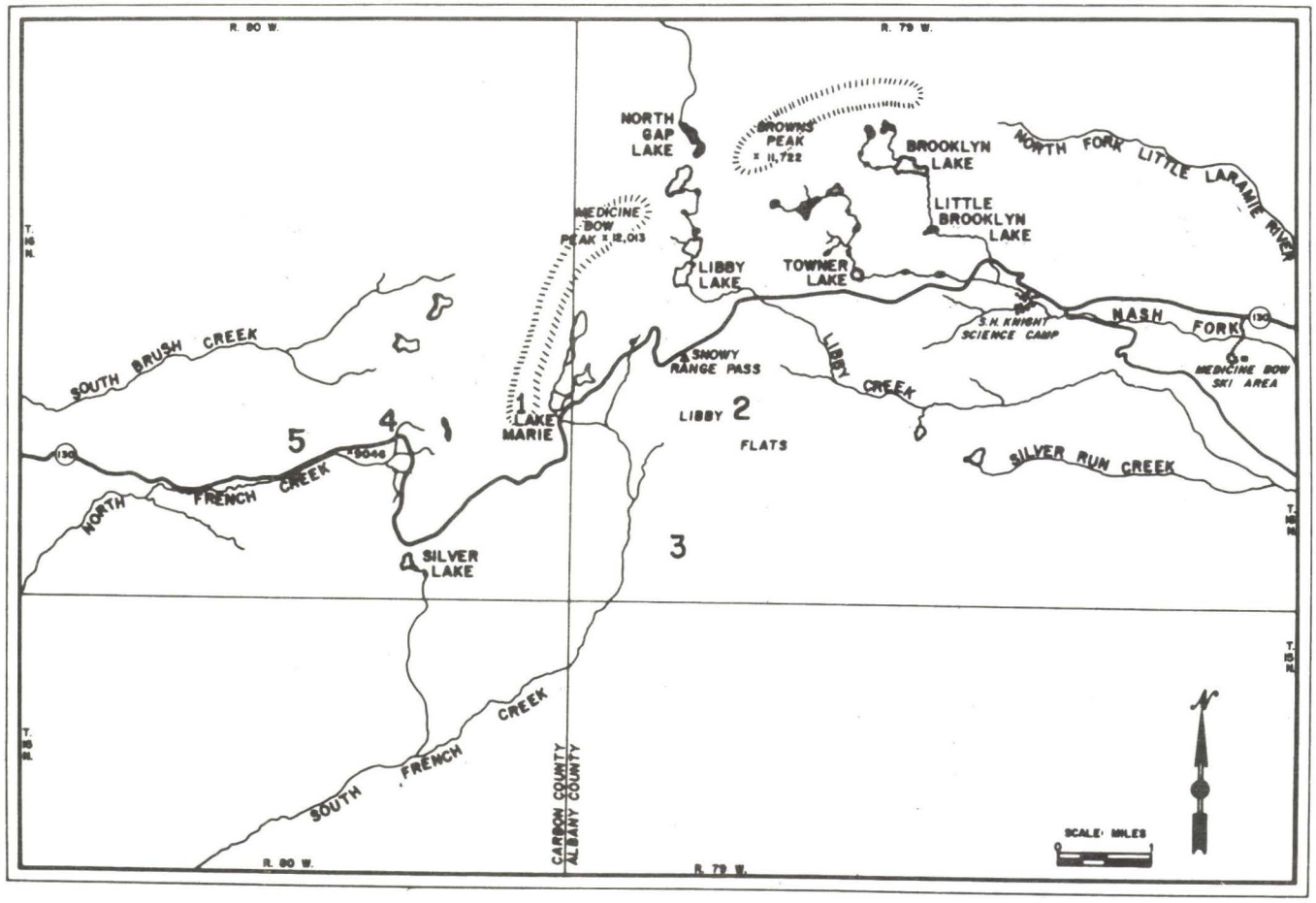

Fig. 6. Approximate location of the 5 study areas used for monitoring certain environmental characteristics (see Table 5 also). Lake Marie (1), Libby Flats (2), Fourlog Park (3), Headquarters Park I (4), and Headquarters Park II (5).

TABLE 5. Location, elevation, and community type of the 5 sites where microclimatic characteristics were measured.

Site Name	Elevation (m)	Community Type	Location
Lake Marie	3,460	alpine tundra	Center of Sec 13, R80W,T16N
Libby Flats	3,230	alpine tundra	NW¼,NW¼,Sec 29, T16N,R79W
Fourlog Park	3,140	mesic subalpine meadow	SW¼,NE¼,Sec 5, T15N,R79W
Headquarters Park I	3,109	dry subalpine meadow	NW¼,NW¼,Sec 26, T16N,R80W
Headquarters Park II	3,054	mesic subalpine meadow	SW¼,NW¼,Sec 27, T16N,R80W

Results

Snow accumulation. An average snow depth of 176 cm was observed in mid-May at the Fourlog Park site. An average of 36 cm of snow depth was lost between 5/15/73 and 5/25/73 at this site, but there was still an average of 39 cm of snow on 6/21/73. By 6/29/73, most of the snow was gone from Fourlog Park, with some snowbanks persisting in shaded locations until after 7/1/73.

Snow accumulation was much greater than expected at the Lake Marie site where an average of 126 cm of snow was present on 5/15/73. Two of the 2 m high posts were completely covered on 5/15/73. These two units did not appear to be in sheltered locations, but did occupy slightly concave microtopographic sites. One sample unit at Lake Marie remained almost snowfree throughout the winter while another became snowfree on 6/22/73.

Snow accumulation at the Libby Flats site was much more typical of windswept alpine tundra. Average snow depth on 5/15/73 was only 28 cm. Most of the units had only 10 cm of snow left on 5/25/73 and all were free of snow by 6/4/73. However, in spite of the lack of snow accumulation at the Libby Flats site itself, the site is not especially xeric.

Because of scattered krummholz, large snow drifts (ca 3-5 m deep) occur approximately 50-70 m to the south and slightly upslope from the site. Snowmelt water from these drifts irrigates the site during late May and early June. The pattern of snowmelt water irrigation is analogous to that described by Billings and Bliss (1959). At 0800 hrs in late May the site was covered by a sheet of ice from the previous days water. By 1000 hrs this ice was melting and water was starting to flow over the surface. By 1200 hrs the ground surface was completely covered with water to a depth of 2-5 cm. The strong surface flow continued until mid-afternoon (ca 1600 hrs). It was much abated by 1800 hrs and ice began to form at this time. The surface flow phenomena seemed to terminate rather abruptly on or about the first week in June, although free water was present at -20 cm in many of the soil sample holes dug on 6/20/73. This diurnal irrigation process did not occur at either Lake Marie or Fourlog Park.

Snow duration at Headquarters Park was 2-3 days longer on the upper Site I. In 1973 Headquarters Park I and II were snow free by June 29 and July 1, respectively, whereas in 1974 they were snow free on June 19 and June 22, respectively. The earlier snow-free dates in 1974 are interesting since that year on May 1 there was about 18 cm more snow water at a nearby snow course than in 1973. Starr (1974) studied 50 meadows in the Headquarters Park area, and found that the snow release date varied from June 22 to July 5 in 1973.

Summer Precipitation. Precipitation recorded during the June to August sample period was much greater in 1973 (June 6 -- Aug. 29) than in 1972 (June 13 -- Aug. 21) (Table 6). The 1973 increase was 3.1 times that at Libby Flats, 2.8 times that at Lake Marie and 2.7 times that at Fourlog Park. On Libby Flats 82 mm of precipitation were recorded between July 19 and August 1, 1973. During this same period 61 mm of precipitation were recorded at Lake Marie and 76 mm at Fourlog Park. Precipitation declined somewhat at all sites during late August 1973.

The 2 sites at Headquarters Park received more precipitation than the higher elevation sites, 130 mm in 1972 and 190 mm in 1973 between July 5 and September 22, Fig. 7.

TABLE 6. Environmental characteristics during the growing season at Libby Flats, Lake Marie, and Fourlog Park in 1972 and 1973.

Sample site	Sample period	Solar radiation (ly)	Wind speed (km/hr)	Total precip. (mm)	Air temperature @ +20 cm (0°C)			Rel. humidity @ +20 cm (percent)			Saturation def. @ +20 cm (mm Hg)		
					Max.	Av.	Min.	Max.	Av.	Min.	Min.	Av.	Max.
	1972												
Libby Flats	6/13 - 6/26	463	35.2	15.0	13.0	6.9	0.8	86	66	45	0.4	3.5	6.5
	6/27 - 7/10	522	39.9	7.9	15.4	8.2	1.0	87	60	40	0.3	3.6	6.9
	7/10 - 7/24	504	50.1	2.8	17.7	9.9	2.1	86	60	34	0.6	5.1	9.5
	7/25 - 8/07	433	40.6	21.8	18.1	10.9	3.7	86	62	37	0.5	5.0	9.5
	8/08 - 8/21	363	29.1	15.5	18.6	11.0	3.4	85	60	36	0.6	5.6	10.5
Lake Marie	6/14 - 6/27	494	25.7	3.8	11.2	6.7	2.2	83	66	48	0.5	3.0	5.4
	6/28 - 7/11	537	36.1	4.8	14.4	7.4	3.5	81	63	45	0.8	3.4	5.9
	7/12 - 7/25	553	48.5	3.8	16.3	10.7	5.0	82	62	41	0.9	4.1	7.2
	7/26 - 8/08	428	30.9	18.8	15.5	10.2	4.9	83	64	45	0.7	4.0	7.2
	8/09 - 8/22	355	25.9	23.4	15.6	10.3	5.0	80	63	45	1.3	4.4	7.4
Fourlog Park	6/15 - 6/28	No sample, site still covered by snow											
	6/29 - 7/12	437	12.6	7.6	17.6	9.3	1.0	90	63	36	0.3	4.4	8.5
	7/13 - 7/26	497	15.9	1.5	19.8	11.4	2.9	91	62	33	0.1	5.1	10.1
	7/27 - 8/09	437	10.0	21.6	19.9	11.3	2.7	91	63	34	0.1	5.1	10.1
	8/10 - 8/23	328	5.6	18.0	18.8	10.8	2.7	90	63	36	0.2	5.2	10.2
	1973												
Libby Flats	6/06 - 6/20	269	23.2	0.3	9.6	4.4	-0.8	83	63	43	1.0	3.0	5.0
	6/21 - 7/04	567	14.0	6.4	16.4	9.6	2.7	80	59	38	1.3	4.8	8.2
	7/05 - 7/18	242	9.4	21.3	16.0	9.5	2.9	86	68	50	0.9	4.0	7.1
	7/19 - 8/01	443	9.0	82.0	13.3	7.4	1.4	91	71	51	0.5	2.9	5.3
	8/02 - 8/15	449	13.3	22.1	16.0	9.6	3.2	81	62	42	1.1	4.3	7.4
	8/16 - 8/29	339	12.2	15.8	17.0	10.8	4.5	88	65	41	0.5	4.4	8.2
Lake Marie	6/07 - 6/21	No sample, site still covered by snow											
	6/22 - 7/05	438	14.8	2.3	13.9	9.7	5.4	73	61	49	1.7	3.7	5.7
	7/06 - 7/19	464	9.6	22.1	13.8	9.3	4.8	87	73	58	0.7	2.7	4.7
	7/20 - 8/02	496	9.0	61.2	11.4	7.0	2.6	88	71	54	0.3	2.3	4.2
	8/03 - 8/16	525	14.2	37.1	13.7	9.0	4.3	75	61	47	1.6	3.7	5.8
	8/17 - 8/30	459	13.3	21.6	14.5	9.9	5.3	85	67	48	0.6	3.2	5.7
Fourlog Park	6/08 - 6/22	No sample, site still covered by snow											
	6/23 - 7/06	136	3.2	4.1	19.7	11.3	2.9	86	57	27	0.6	6.5	12.4
	7/07 - 7/20	289	2.3	20.3	15.9	9.5	3.1	92	73	53	0.1	3.2	6.3
	7/21 - 8/03	128	0.6	75.7	15.6	8.4	1.2	92	67	42	0.2	3.4	6.6
	8/04 - 8/17	455	1.6	24.1	17.7	10.3	2.9	89	64	39	0.2	4.5	8.7
	8/18 - 8/31	335	0.5	6.9	18.6	11.2	3.7	89	62	35	0.2	4.6	8.9

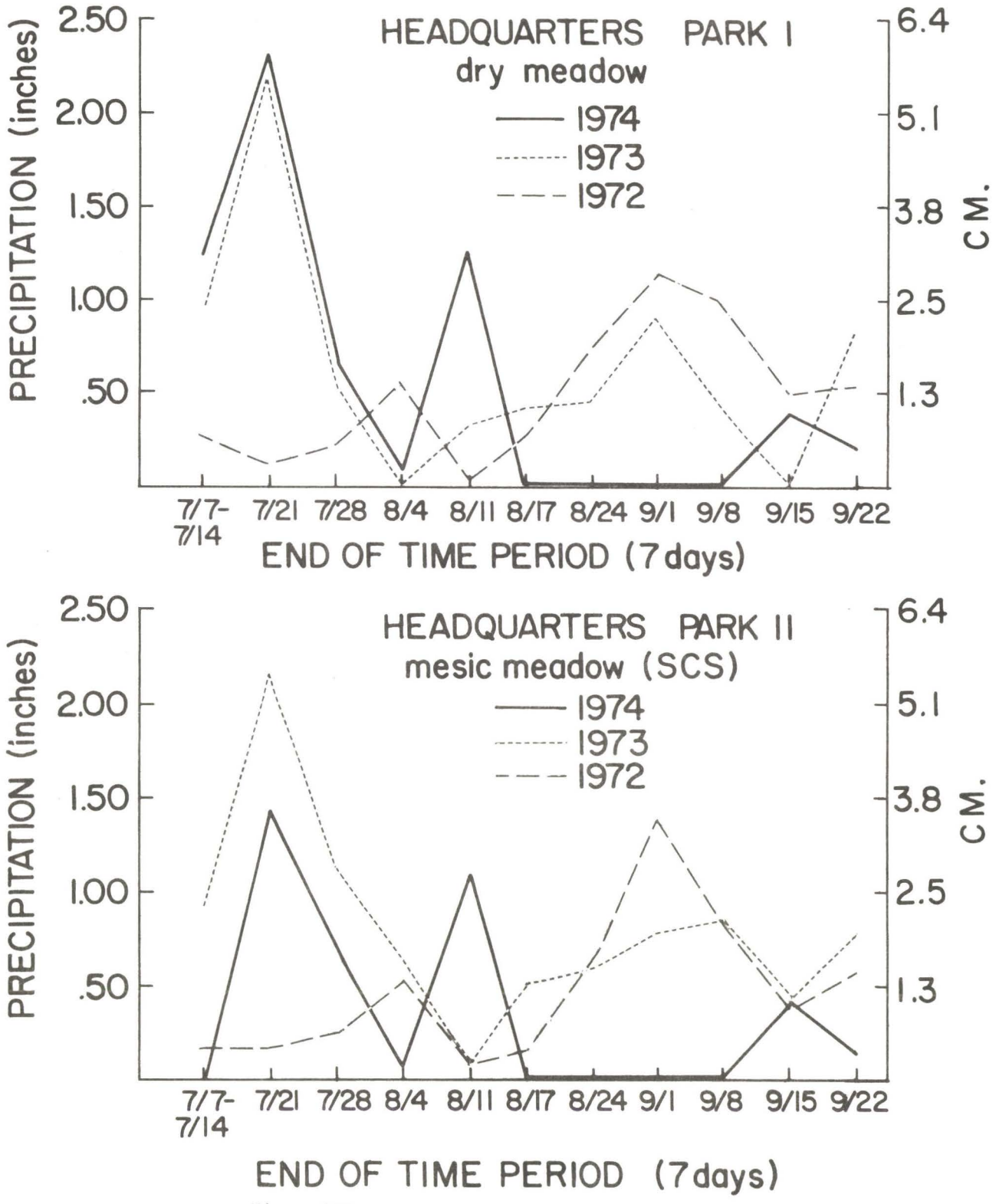

Fig. 7. Distribution of summer precipitation in 1972, 1973, and 1974 at two sites in Headquarters Park.

Relative Humidity and Saturation Deficit. Highest values of relative humidity were recorded at Fourlog Park where night time values were often 100%, Table 6. Maximum relative humidity at Lake Marie was slightly lower than at Libby Flats, but minimum relative humidity values were higher and Lake Marie had the lowest range in relative humidity of the three upper sites.

Saturation deficits are inversely related to relative humidity (Table 6). As would be expected, higher saturation deficits occurred in 1972, the dryer year. Average season-long saturation deficits at Fourlog Park were: 1972, 5.0 mm Hg; 1973, 4.5 mm Hg. These were slightly higher than the saturation deficits at Libby Flats (1972, 4.6 mm Hg; 1973, 3.8 mm Hg) or at Lake Marie (1972, 3.7 mm Hg; 1973, 3.1 mm Hg). Bliss (1956) reported average values of 8.9 to 10.9 mm Hg for other alpine sites in the Medicine Bow Mountains.

Afternoon saturation deficit data for the 2 sites at Headquarters Park were similar to the 3 upper sites, Fig. 8. The 2 sites did not differ greatly and by mid-August the difference between 1972 and 1973 was very slight. Prior to mid-August the 1973 deficit values were considerably less, a reflection of the cooler, wetter weather. Relative humidity ranged from 45 to 80%.

Soil Moisture. The average moisture content of the soil at the 3 upper sites was 7 to 10% higher in 1973 than in 1972 (Table 7). Highest soil moisture occurred at Lake Marie and lowest at Fourlog Park, Table 7. In 1972, the average soil moisture was below 10% at Fourlog Park in early July. It increased only slightly at the time of the late July-August precipitation increase. A similar increase in soil moisture was recorded at the other two sites in 1972, with that at Lake Marie being the greater. Early season soil moisture exceeded 40% at Lake Marie in 1972 and 1973, and at Libby Flats in 1973. Average season-long values for 1972 and 1973, respectively, were Libby Flats, 21% and 30%; Lake Marie, 28% and 35%; and Fourlog Park, 12% and 22%.

The general trend in soil moisture was downward at all sites in 1973, with the exception of a slight increase (1.1%) at Libby Flats during the July 19 to August 1 period when 82 mm of precipitation were recorded. No increase occurred at Fourlog Park in response to the 76 mm

of precipitation recorded there during the same period, or at Lake Marie where 61 mm were recorded. It seems clear that very little soil moisture recharge occurs from summer precipitation, an observation made also by Reynolds and Knight (1973).

Starr (1974), in his study of the Headquarters Park meadows, observed three distinctive soil moisture patterns that are illustrated in Fig. 10. Wet meadow soils remained saturated at least until August 25; mesic meadows were saturated until about July 26, after which they dried to as low as 40 to 50 percent; and dry meadows were down to 20 to 50 percent soil moisture by mid-July.

Solar radiation. The incoming solar radiation regime at Lake Marie was very similar during the 1972 and 1973 sample period (Table 6). The daily averages for the period were 468 ly in 1972 and 476 ly in 1973. This is about 64 to 65% of the average maximum clear-sky incoming solar radiation of 727 ly.

At Libby Flats and Fourlog Park incoming solar radiation was 10 to 20% less in 1973 as compared to 1972 (Table 6). The Fourlog Park site had an average of only 278 ly or 38% of the possible clear-sky incoming solar radiation; the Libby Flats site had an average of 408 ly or 56% of the possible.

The reduction in 1973 of incoming solar radiation was caused by a greater incidence of cloudiness. In 1972 the pattern of cloudiness for all sites was generally controlled by orographic lifting. Clear skies were present to about 1200 hours after which the cloud cover increased to about 1800 hours, then dissipated to some extent prior to sunset (ca 2000 hrs). The afternoon cloudy period was sometimes accompanied by thundershower activity. In 1973, on the other hand, there was more frontal activity and the cloud cover remained for several days at a time. This different weather pattern is reflected in the increased precipitation recorded in 1973.

Wind. High winds are a characteristic feature of alpine environments. Libby Flats was the windiest site in 1972 with an average wind speed of 39 km/hr for the June through August sample period (Table 6). Lake Marie was slightly less windy, the average being 33.4 km/hr.

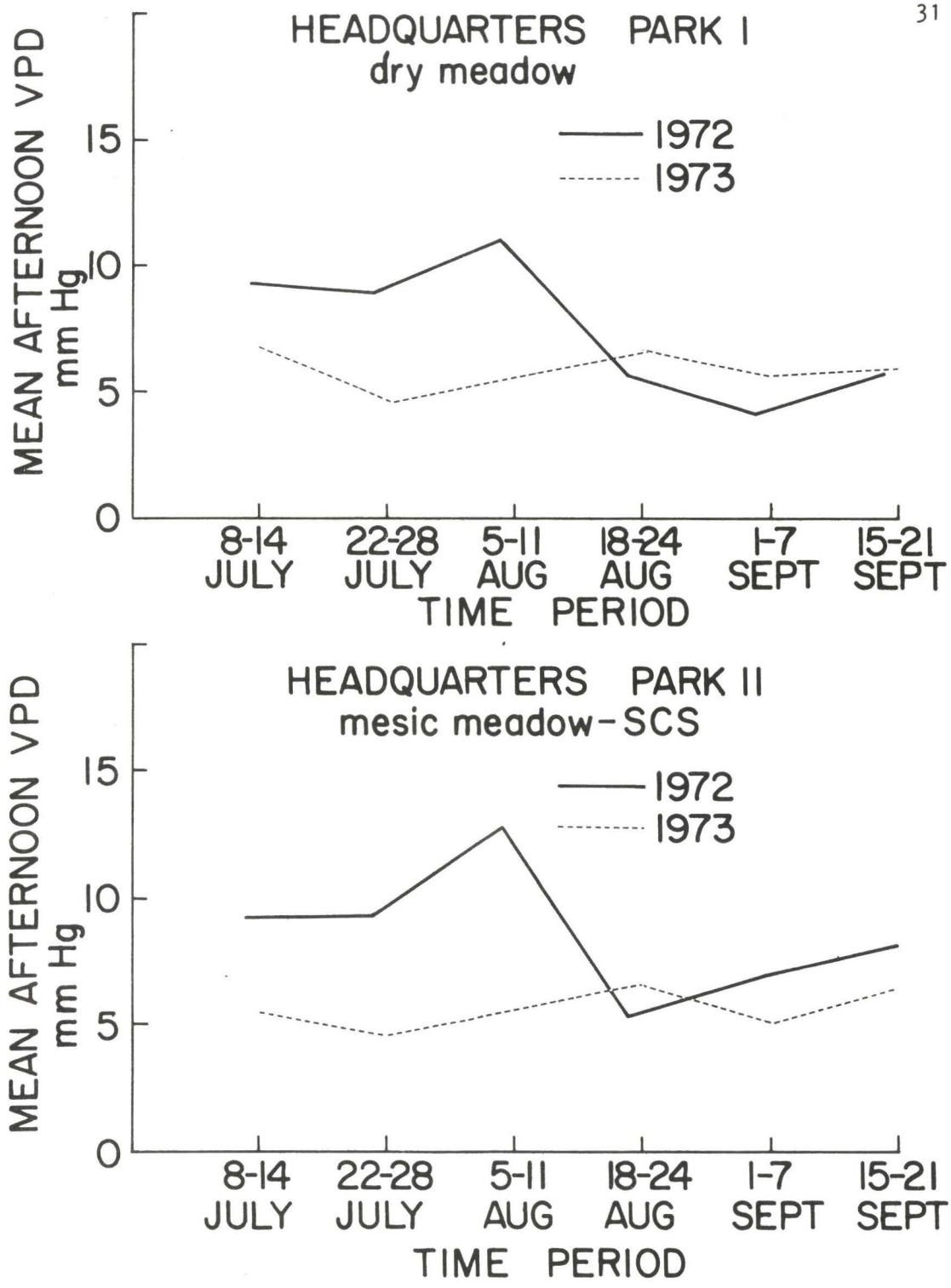

Fig. 8. Variation in afternoon vapor pressure deficit during the period of mid-July to mid-September at two sites in Headquarters Park.

Average wind speed at the sheltered, subalpine Fourlog Park site was 11.0 km/hr in 1972.

In 1973 wind speed was much reduced at all of the 3 upper sites. Libby Flats still had the greatest average wind speed (13.5 km/hr), but this was 2.6 times less than the previous year. Wind at Lake Marie averaged 12.2 km/hr, or 2.7 times less than 1972, and Fourlog Park had an average wind speed of only 1.6 km/hr. This was almost 7 times lower than in 1972. Part of the reduction in wind speed at Fourlog Park in 1973 might have been caused by the increased height of the plant canopy. In 1972, when the anemometers were installed, the plant canopy only grew to about 25 cm in height. In 1973, the plant canopy was 40 to 45 cm tall. Since the anemometer cups were at 50 cm above the ground surface, the relative effect of the increased plant height would be to lower the wind speed at the 50 cm height. The reduction of wind speed with decreasing distance to the relative surface is well documented (Geiger 1959).

Air Temperature. Average air temperatures at all sites in 1973 were lower than in 1972 (Table 6), probably a result of the more frequent cloudy, wet weather.

Of the upper sites, the greatest diurnal range in air temperature occurred at Fourlog Park. This site is much more sheltered than the other two sites and nocturnal cold air drainage is a common phenomena. Two of the temperature sensors at Fourlog Park frequently had nighttime minimum air temperatures of $0^{\circ}C$. These were slightly lower on the slope than the other three units. Conversely, the sheltered location and lack of wind caused daytime air temperature at Fourlog Park to be warmer than at the other two sites. The average daytime air temperature at Fourlog Park was $19.0^{\circ}C$ in 1972 and $17.5^{\circ}C$ in 1973. This is from 2.4 to $2.6^{\circ}C$ higher than at Libby Flats and 4.4 to $4.0^{\circ}C$ higher than at Lake Marie.

Average air temperatures of 8.5°, 9.0°, and $10.2^{\circ}C$ were recorded at Libby Flats, Lake Marie, and Fourlog Park, respectively, in 1973.

Fig. 9 summarizes afternoon air temperature at the 2 sites at Headquarters Park. Freezing temperatures were recorded at both sites

during June, July, and August, and maximum daytime temperatures were 18 to 21°C.

Soil Temperature. Table 7 summarizes soil temperature data for the Libby Flats site in 1972. The -5 cm level had the highest average temperature (5.7°C) and the greatest diurnal range in temperature (5.4°C) as compared to the two lower levels. The average soil temperature at -20 cm was only 0.3°C less than that at -5 cm, but the range was only 3.3°C. At 50 cm, the average was 3.6°C with only a 0.8° range. In 1973, despite the generally cooler and wetter weather, the average soil temperature at -5 cm was higher by 4.1°. Both seasonal maximum and minimum temperatures were higher and the range was also greater (6.7°C). However, soil temperatures at the two lower levels were cooler in 1973 than in 1972 (3.8°C at -20 cm; 9.2°C at -50 cm). The range in temperature was also lower, being only 1.1°C at -20 cm and 0.8°C at -50 cm.

Soil temperatures at Lake Marie in 1973 were the coolest of all the sites. Seasonal averages at -5 cm were 4.4°C with a 5.5° range; at -20 cm, 2.8°C with a 1.0° range; and at -50 cm, 3.4°C with a 0.8° range. An increase in soil temperature at the -50 cm depth also occurred at Fourlog Park, but not at Libby Flats. The average soil temperature at -5 cm at Fourlog Park in 1973 was slightly lower than that at Libby Flats (9.2°C vs 9.8°C). The greater height of the vegetation at Fourlog Park would provide a more shaded soil surface and perhaps reduce the soil temperatures in the upper part of the solum. The generally cooler nighttime air temperature would also influence shallow soil temperatures. Deeper subsurface soil temperatures at Fourlog Park were the highest of all three sites. At -20 cm the average was 6.8°C with a range of 2.9°C; at -50 cm the average was 7.9°C with a range of 2.8°C. As can be seen the soil temperature range at the two lower levels was greater at Fourlog Park than at the other sites.

Starr (1974) collected soil temperature data from 50 stands in Headquarters Park, and observed a range from 7.8°C to 25.0°C at -5 cm, which is warmer than the higher elevation sites. The warmest temperatures were observed most frequently on July 11. Soil temperature at -20 cm varied from 6.4°C to 17.8°C, with no one date being generally warmer.

TABLE 7. Average soil temperature and soil moisture for 14-day periods during the growing seasons of 1972 and 1973.

Sample site	Sample period	Soil temperature (°C)									Soil moisture (%)
		-5 cm			-20 cm			-50 cm			
		Max.	Av.	Min.	Max.	Av.	Min.	Max.	Av.	Min.	
	1972										
Libby Flats	6/13 - 6/26	- - - - - - - Thermograph not in operation - - - - - - -									36.2
	6/27 - 7/10	6.1	4.1	2.1	3.4	2.8	2.1	2.6	2.3	1.9	21.0
	7/11 - 7/24	5.7	4.2	2.6	4.8	4.5	4.1	5.1	4.6	4.1	14.2
	7/25 - 8/07	11.2	7.5	3.7	.56	5.0	4.4	4.7	4.3	3.9	16.2
	8/08 - 8/21	10.5	7.1	3.7	5.8	5.1	4.3	3.7	3.3	2.8	18.7
Lake Marie	6/14 - 6/27	- - - - - Thermograph not installed in 1972 - - - - - -									43.4
	6/28 - 7/11										33.7
	7/12 - 7/25										23.0
	7/26 - 8/08										14.7
	8/09 - 8/22										26.1
Fourlog Park	6/15 - 6/28	- - - - - Thermograph not installed in 1972 - - - - - -									NA
	6/29 - 7/12										16.3
	7/13 - 7/26										9.9
	7/27 - 8/09										10.7
	8/10 - 8/23										12.5
	1973										
Libby Flats	6/06 - 6/20	10.0	6.7	3.4	1.2	0.7	0.2	0.2	0.1	-0.1	45.6
	6/21 - 7/04	16.1	12.0	7.9	5.0	4.4	3.7	2.7	2.2	1.7	31.5
	7/05 - 7/18	14.7	11.2	7.6	5.2	4.6	3.9	4.1	3.6	3.1	28.6
	7/19 - 8/01	14.1	10.8	7.4	5.3	4.8	4.2	4.4	3.9	3.3	29.7
	8/02 - 8/15	16.0	12.1	8.1	6.2	5.6	5.0	5.3	5.0	4.6	25.7
	8/16 - 8/29	7.6	5.8	4.0	3.0	2.7	2.4	5.1	4.7	4.2	18.8
Lake Marie	6/07 - 6/21	- - - - - - - Thermograph not in operation - - - - - -									NA
	6/22 - 7/05	2.1	1.4	0.7	0.8	0.6	0.4	0.4	0.4	0.3	43.1
	7/06 - 7/19	8.1	4.9	1.7	3.6	3.0	2.4	3.3	2.9	2.5	LS[1/]
	7/20 - 8/02	7.1	3.8	0.5	3.2	2.5	1.8	4.0	3.5	2.9	37.7
	8/03 - 8/16	9.3	5.7	2.1	4.6	4.0	3.4	5.5	4.9	4.7	31.0
	8/17 - 8/30	8.9	5.9	2.8	4.3	4.3	3.6	5.6	5.0	4.4	29.2
Fourlog Park	6/08 - 6/22	- - - - - - - Thermograph not in operation - - - - - -									NA
	6/23 - 7/06	16.9	10.5	4.1	8.6	6.5	4.4	7.2	5.5	3.8	20.7
	7/07 - 7/20	14.2	9.8	5.3	8.9	7.4	5.9	9.7	8.4	7.1	28.9
	7/21 - 8/03	10.1	6.6	3.1	6.3	5.1	3.8	8.1	6.9	5.6	23.2
	8/04 - 8/17	13.7	9.3	4.9	8.6	7.2	5.8	10.6	9.2	7.7	16.2
	8/18 - 8/31	14.8	10.0	5.2	8.8	7.6	6.4	10.9	9.5	8.1	10.7

[1/] LS = Sample lost in fire

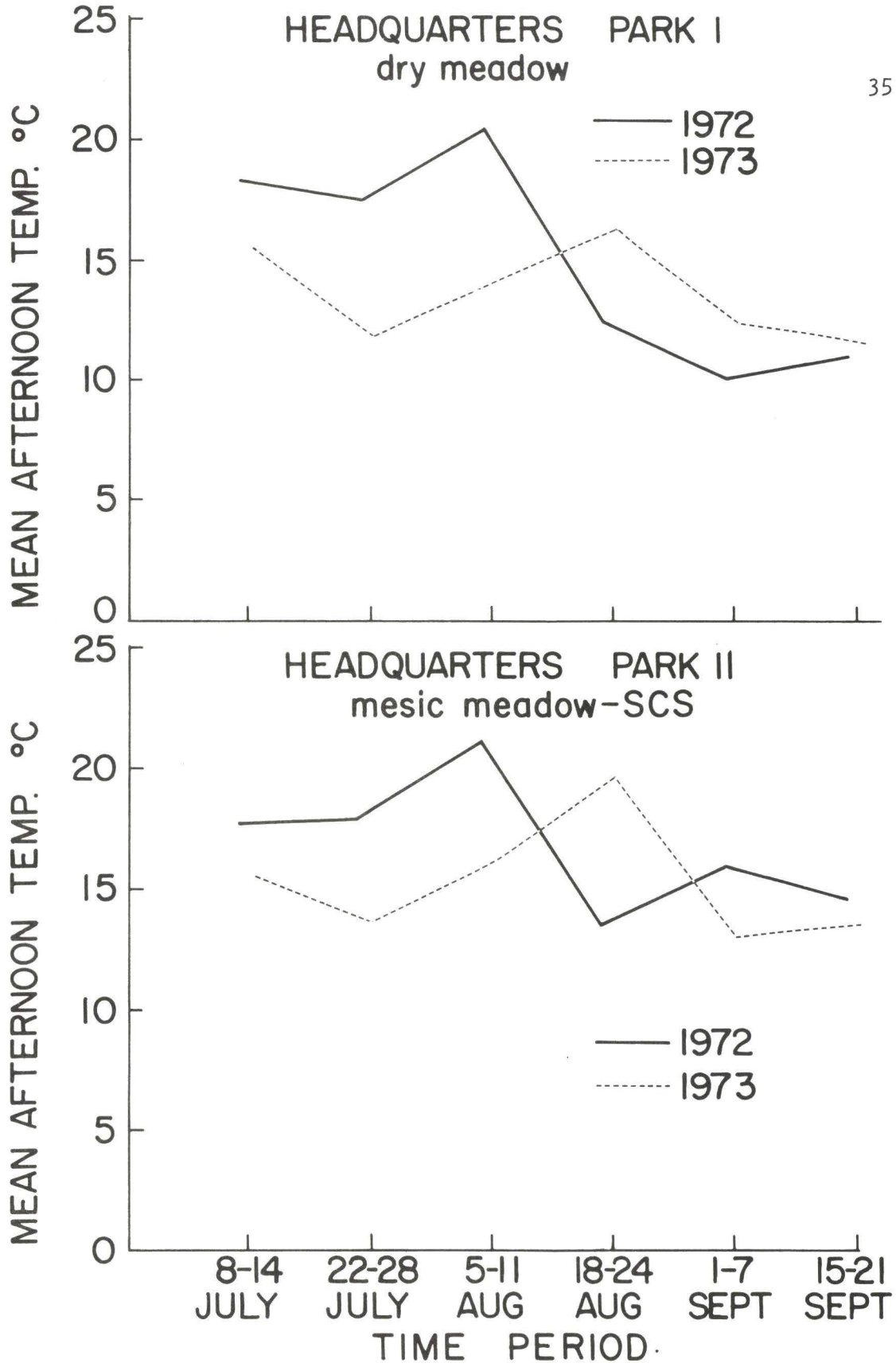

Fig. 9. Variation in afternoon temperature during the period of mid-July to mid-September at two sites in Headquarters Park.

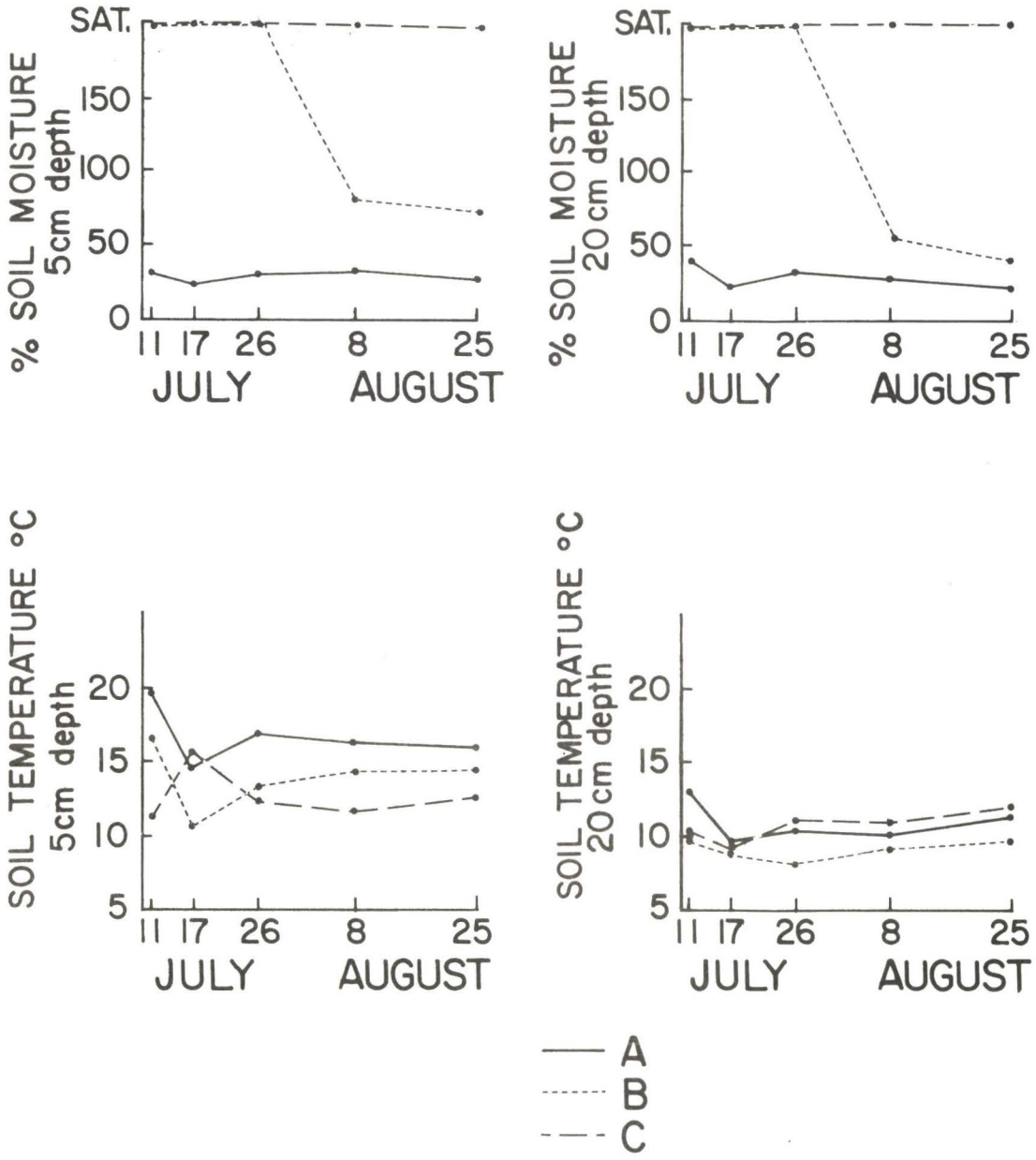

Fig. 10. Variation in soil moisture (-5 cm and -20 cm) and soil temperature (-5 cm and -20 cm) at a dry meadow (A), mesic meadow (B), and wet meadow (C) in Headquarters Park.

Seasonal trends in soil temperature for 3 of Starr's stands are illustrated in Fig. 10.

Because soil temperature is easily measured and serves to integrate various climatic characteristics, it would be a useful parameter to monitor continuously in order to evaluate climatic change.

VEGETATION ECOLOGY

Dennis H. Knight and John Thilenius

Beginning with the explorations in the early 1900's of Ramaley, Cary, Rydberg, Shantz, Clements, and Nelson, information has been accumulating on the vegetation ecology of the Medicine Bow Mountains and the Rocky Mountains in general. In 1934, Hanna published the first description of the plant communities in one section of the mountains, but even before then, in 1912, Douglas had produced a vegetation map for most of the Medicine Bow Mountains for the U. S. Forest Service. The Forest Service has since then completely re-mapped the mountains in considerable detail using aerial photographs. Both the Forest Service and the University of Wyoming Remote Sensing Laboratory have good collections of aerial photographs for the Medicine Bow Mountains, so that future shifts in vegetation boundaries can be observed.

The vegetation of the mountains has probably not changed much since glaciers moved down the slopes of Medicine Bow Peak over 8,000 years ago. The pollen record is not well studied, but it seems reasonable now to assume that lodgepole pine (Pinus contorta Dougl.), aspen (Populus tremuloides Michaux), and Engelmann spruce (Picea engelmannii Parry) invaded the till as the glaciers retreated. Today these same tree species dominate the forest vegetation, along with subalpine fir (Abies lasiocarpa (Hook.) Nutt.) which has been in the mountains also since before Pleistocene glaciation.

Following glaciation, the most frequent disturbance for thousands of years was fire, caused both by lightning and the native American Indian. Evidence of fire is abundant, and lodgepole pine seems to depend on periodic fire for its existence. Billings (1969) studied old

stumps on Libby Flats, and concluded that much of the Flats were forested previous to fires in 1766, 1774, and 1809. Libby Flats is now a wind-swept subalpine meadow (partially tundra) in which spruce are invading very slowly as islands of krummholz.

Other forest fires of note occurred in the 1860's, some perhaps being started by the Indians in defiance of the Union Pacific Railroad being built through the Laramie Basin. On September 8, 1871 the Laramie Daily Sentinel reported that the Mountains could not be seen from the city for a 2-month period due to the smoke from forest fires. These fires undoubtedly favored the development of pioneer forests dominated by lodgepole pine and aspen, and they probably served also to keep the native mistletoe in check. Some forests did apparently go unburned, for example the spruce-fir natural area above Science Camp where Engelmann spruce have been aged at 500 years old. All of the tree species above 2740 m elevation are relatively intolerant to fire, unlike ponderosa pine (Pinus ponderosa Laws.) at the lower elevations.

Fires are still frequent in the Medicine Bow Mountains, but every effort is made to control them immediately. It is interesting to speculate whether the control of fire has in fact changed the Medicine Bow ecosystems more than a 15 percent increase in snowfall would.

Logging activity first became noticeable when the railroad was extended into the vicinity about 1868. Selected trees of about 35 cm diameter were cut for railroad ties, a practice known as "tie-hacking." Today logging is the major industry in the mountains, and a conspicuous one as well since the clear-cutting method seems well suited for the most abundant and most valuable species, lodgepole pine. Whether or not clear-cuts adequately simulate fires in the forest ecosystem is still being debated, but certainly logging activities have replaced fire as the major source of ecosystem perturbation. Wind storms are occasionally

important. Grazing of the forest ecosystems seems to have had a minor influence, but some of the alpine meadows may have been affected by sheep. Dwarf mistletoe causes considerable perturbation to the lodgepole forest ecosystem in The Medicine Bow Mountains, but thus far the pine beetle has not been a serious problem.

The forests of the Medicine Bow National Forest have been classified recently by Wirsing (1973). He recognizes and discusses the following habitat types:

1. Ponderosa pine forest (Pinus ponderosa -- Carex geyeri)
   a. Lupine phase (Lupinus argenteus)
   b. Stonecrop phase (Sedum lanceolatum)

*2. Aspen forest (Populus tremuloides -- Carex geyeri)**

*3. Subalpine fir -- Engelmann spruce -- broom huckleberry forest (Abies lasiocarpa -- Picea engelmannii -- Vaccinium scoparium)
   a. Sibbaldia -- Bistort phase (Sibbaldia procumbens -- Polygonum bistortoides)

*4. Subalpine fir -- Engelmann spruce -- elk sedge forest (A. lasiocarpa -- P. engelmannii -- Carex geyeri)

5. Limber pine --spike fescue woodland (Pinus flexilis -- Leucopoa kingii)
   a. Pasque flower phase (Anemone patens (Pulsatilla ludoviciana))
   b. June-grass phase (Koeleria cristata)

The extensive lodgepole pine forests are not recognized by Wirsing (1973) as a habitat type because he believes they are always successional to the Abies-Picea type. Moir (1969), Patterson and Knight (unpublished data), and others do not agree with this contention, and believe that a lodgepole pine habitat type should also be recognized. Fig. 11 shows the altitudinal distribution of the 3 major tree species in the Nash Fork Creek watershed of the Medicine Bow Mountains.

Other terrestrial vegetation types in the Medicine Bow Mountains include the alpine tundra, subalpine meadows of various types and the foothill sagebrush-grassland. Nelson (1974) has just completed a new flora for the Mountains.

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* Those habitat types marked with an asterisk are especially common in the Medicine Bow Mountains.

** Gartner (1967) observed that aspen was found most frequently on Elk Mountain where snow accumulates.

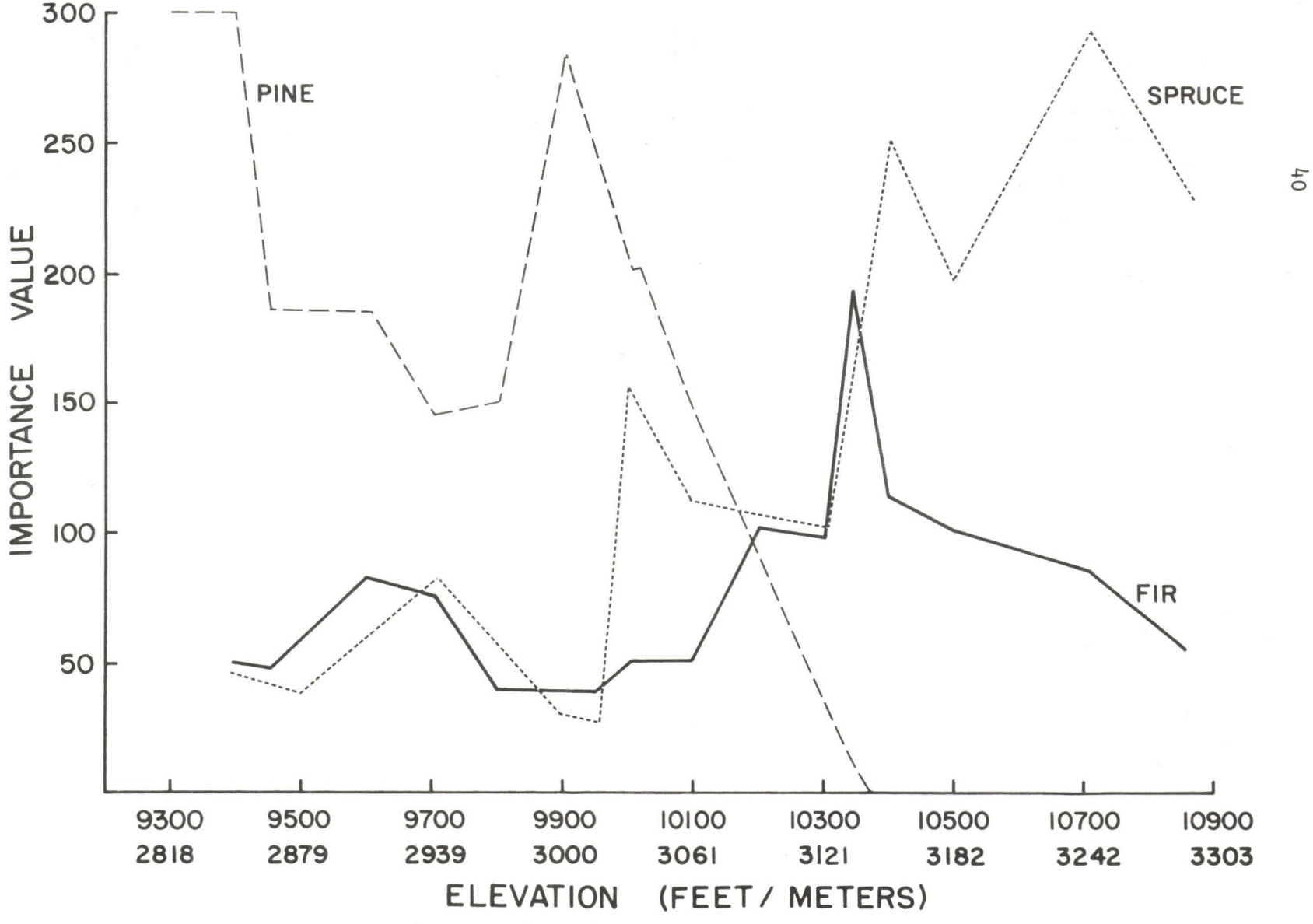

Fig. 11. The importance value of 3 tree species in the Nash Fork Creek watershed in relation to elevation. Importance value equals relative density plus relative frequency plus relative basal area. Source: unpublished data.

Considerable autecological information is available for the trees of the Medicine Bow Mountains, too much to be summarized in this report. A few observations, however, are relevant particularly to precipitation management. First, with regard to moisture requirement, Engelmann spruce, subalpine fir, and aspen seem most demanding when in the seedling stage. Mature trees can tolerate considerable stress, but seedling establishment is the critical phase of the life cycle. Lodgepole pine, Douglas fir, ponderosa pine, and limber pine are believed to require less moisture. Bates (1923) and Swanson (1967) found that spruce use more water than lodgepole pine, and this may explain the restriction of spruce to the more mesic sites. Ronco (1970) decided that seedling establishment of Engelmann spruce is sporadic because often the seed bed is too dry by the time it is warm enough for germination.

Except for lodgepole pine, those tree species requiring the most moisture are also the most abundant in the planned target area, especially Engelmann spruce and subalpine fir. Whether cloud seeding will stimulate or retard the growth of these species will depend on exactly how precipitation management affects the climate and length of growing season, and whether the trees are in fact most limited above 9,000 feet (2740 m) by water availability, soil temperature, length of growing season, or nutrients. Whether seedling establishment is favored would again depend on the actual effects of cloud seeding and on the current limiting factors for seedling establishment on various sites in the mountains. As Waggoner (1966) and Whittaker (1967) have pointed out, a change in the moisture regime could affect rates of succession and community composition; the mechanism is understood only with a knowledge of limiting environmental factors and the actual effects on the environment resulting from precipitation management. Our research was not focused on the trees, but we have studied the limiting factors controlling the forest understory, meadow, and tundra vegetation.

Another characteristic of the coniferous trees at high elevations is their susceptibility to the brown-felt fungi (Herpotrichia nigra Hartig and Neopeckia coulteri (Peck) Sacc.), which grow in snow banks and are known to kill seedlings. It is not uncommon to find seedlings that have

been killed by these fungi, though usually only one or two branches are killed. If cloud seeding results in additional snowbanks that do not melt until mid- or late-June, then a higher incidence of brown-felt fungus disease is possible. Other snow-molds, usually found on the organic matter on the forest floor, are also of concern in this regard (Korstian 1923), though it is not known that they are a problem for seedling establishment in the Medicine Bow Mountains.

Engelmann spruce seedlings above 3,050 m elevation are also known to be subject to solarization, a chlorosis that develops when sunlight is too intense (Ronco 1970). Solarization is a natural phenomenon that may prevent spruce from invading certain habitats, e.g. adjacent to late persisting snow banks which will reflect much of the sunlight. There are no data or observations to indicate that increased winter snowfall would increase the chances of solarization of spruce seedlings in the spring, but the possibility exists. In this regard, it is interesting that Engelmann spruce seedlings reach a maximum photosynthesis rate at 43,056 to 53,820 lumen/m^2 (4,000-5,000 ft. candles), while lodgepole seedlings do not appear light saturated even at 129,168 lumen/m^2 (12,000 ft. candles) (Ronco 1970).

The zonation of the forest vegetation in the Rocky Mountains has been summarized by Moir (1969). He suggests that lodgepole forest is not always a pioneer community, forming a climax on some sites where spruce and fir are unable to grow or where they invade very slowly (Fig. 12). Moir recognizes a climax lodgepole pine forest zone between 2500 and 2835 m elevation in Colorado, and this seems appropriate for the Medicine Bow Mountains where some lodgepole stands appear to be climax also. The elevational delimitation may not be appropriate, however, especially since our observations would agree with others who suggest that slope and exposure have a greater influence on plant distribution than elevation.

Patterson and Knight (unpublished data) in 1972 studied the understory species composition of 25 stands of lodgepole pine forest in relation to elevation and moisture gradients. The stands ranged in elevation from 2500 to 3020 m and were all located on the east slope of the Medicine

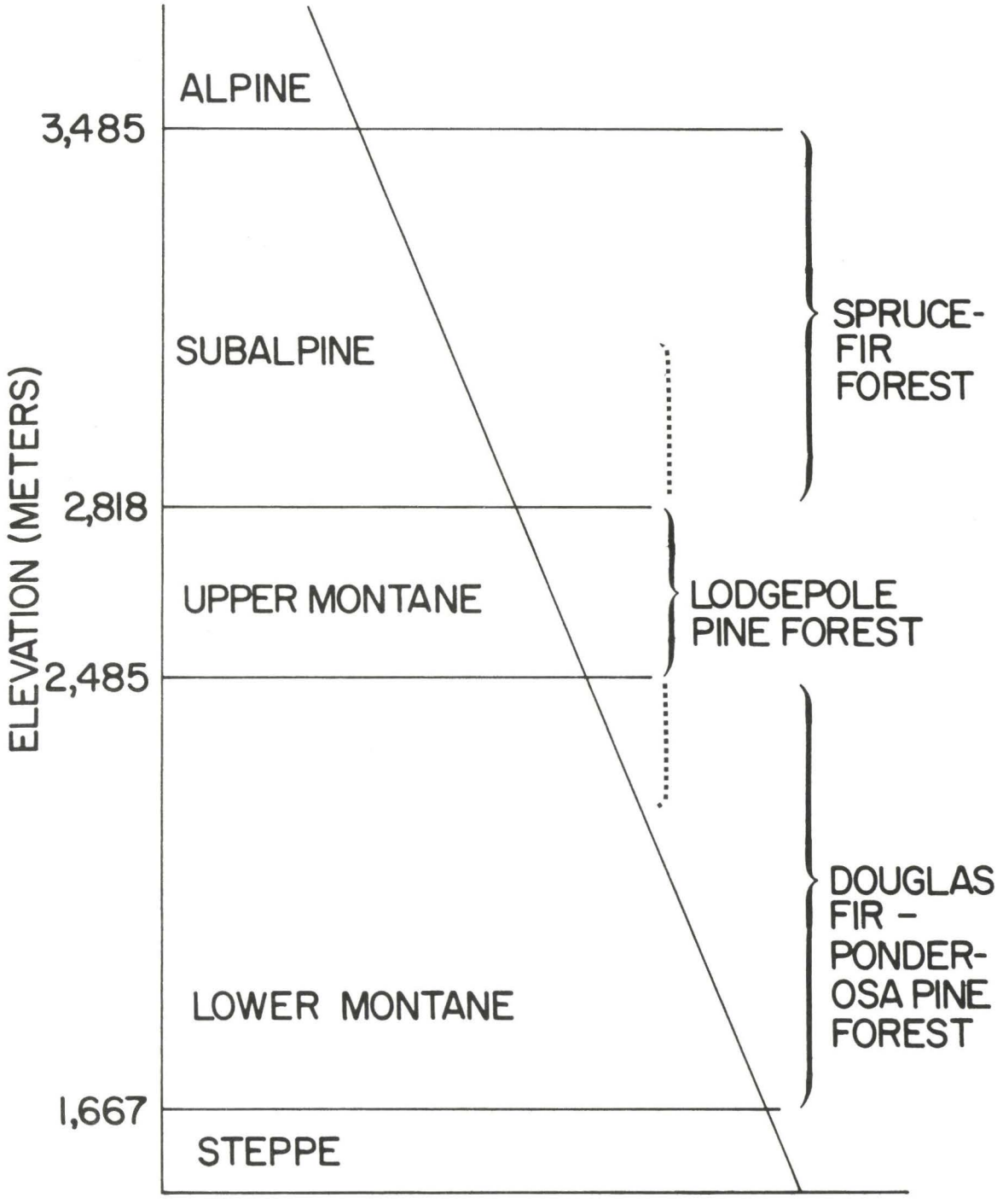

Fig. 12. Vegetation zonation in the Wyoming-Colorado area of the Rocky Mountains (after Moir 1969).

Bow Mountains, between highways 130 and 230. The major understory species in this area and their preferred habitat are as follows:[1]

Higher elevation, mesic sites:

- Abies lasiocarpa saplings
- Fragaria ovalis
- Hieracium albiflorum
- Hieracium gracile
- Lewisia pygmaea
- Picea engelmannii saplings
- Stellaria umbellata
- Vaccinium scoparium
- Zigadenus elegans

Higher elevation, drier sites:

- Juniperus communis
- Solidago spathulata

Lower elevation, drier sites:

- Mahonia repens
- Rosa woodsii
- Shepherdia canadensis
- Lupinus argenteus

Three species were not specific with regard to elevation and moisture -- Arnica cordifolia, Epilobium angustifolium, and Erigeron peregrinus.

Rogers (1974) has described the understory species composition of a lodgepole forest on the west slope of the Medicine Bow Mountains. In addition to the above species, he frequently encountered the following: Astragalus miser, Calamagrostis rubescens, Carex geyeri, Carex rossii, Chimaphila umbellata, and Pyrola secunda.

Above Moir's lodgepole zone is the subalpine spruce-fir zone, the classical climax for the Rocky Mountains occurring just below timberline. This zone accumulates more snow than any other, to some extent due to snow being blown off from the windswept tundra above. Lodgepole forests occur in this zone also, but they are definitely seral. Stahelin (1943) has summarized the possible successional sequences for subalpine forests following fire in Colorado, and the same sequences seem possible in Wyoming (Fig. 13). Oosting and Reed (1952) have written about the autecology and synecology of the virgin spruce-fir forests of the Medicine

[1] Nomenclature follows Harrington (1954). See Appendix I for common names and authorities.

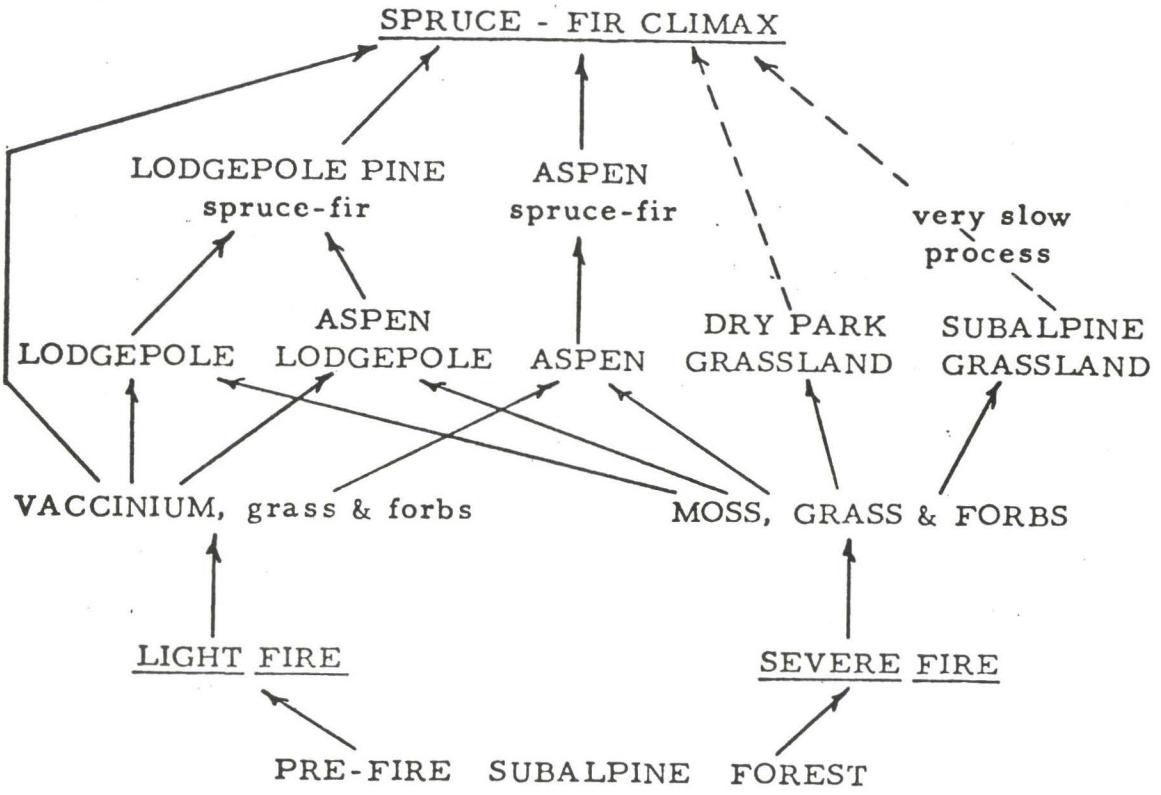

Fig. 13. Predominant secondary successional trends in subalpine forest of the central Rocky Mountains following light and severe forest fires (after Stahelin 1943).

Bow Mountains. They list the following understory species as most characteristic: Vaccinium scoparium, Erigeron peregrinus, Arnica cordifolia, Poa reflexa, Arnica mollis, Pyrola secunda, Pedicularis racemosa, Carex rossii, C. geyeri, Poa nervosa, Thlaspi glaucum. As in many lodgepole pine forests, the small shrub Vaccinium scoparium is by far the most abundant understory species in the spruce-fir forests. Fox (1940) and Stahelin (1943) concluded that the best spruce and fir reproduction and production occurred where V. scoparium had the highest frequency.

Forest net primary productivity in the Medicine Bow Mountains is unknown at this time, except for wood production estimates such as those made for lodgepole pine by the U. S. Forest Service. They estimate that lodgepole wood production in unmanaged stands ranges from a high of about 3.15 m^3/ha/yr to a low of −0.5 m^3/ha/yr. Wood production is greatest when the trees are 12.7 cm to 25.4 cm in diameter (dbh) and on a site of high productive potential. Moir (1972) estimated the annual net above-ground productivity of a 77 year old lodgepole forest in Colorado at 8.4 metric tons per hectare, which is low compared to many other coniferous forests.

Alexander (1974) presents site index curves for the central Rocky Mountains, which show that Engelmann spruce and lodgepole pine may grow 36.6 m and 30.5 m in 100 years, respectively. The maximum growth for both species in the Medicine Bow National Forest is 24.4 m in 100 years according to Wirsing (1973).

Forest productivity in the Mountains is thought to be relatively low, in part due to the short growing season above 2740 m. A higher mean snow accumulation will probably not affect primary productivity unless the growing season is shortened, and additional moisture from cloud seeding will probably not enhance productivity because the soils are believed to be completely saturated anyway just after the melt of normal snow amounts. Work done by Reynolds and Knight (1973) and others suggests that the soil usually dries continuously during the summer, with very little recharge from summer rain. Gary (1974) observed a situation where the radial growth of Engelmann spruce was unaffected by

late persisting snow drifts in New Mexico. In that area, however, the growing season may extend later into the fall than in Wyoming. Hansen (1940) found that fir was more sensitive than spruce to annual fluctuations in climate.

Alexander (1974a, 1974b) has summarized the status of the knowledge about the silviculture of the timber types found in the central and southern Rocky Mountain region. A considerable amount of information on forest disease is available.

Subalpine meadows intermingled with forest are common, especially above 2700 m elevation. Cary (1966) studied a series of forest-meadow margins to determine under what conditions the margins were stable. He found that high snow accumulation, south to southwest exposures, or saturated soils in June were factors associated with stable margins. The forest was tending to invade the adjacent meadow where these conditions did not prevail and where the soils were sandier, cooler, and less saturated in the summer. Winter precipitation management could modify snow accumulation and the duration of soil saturation, but any statement about the likelihood of this happening and the subsequent effect would be weakly supported speculation.

Starr (1974) conducted a detailed phytosociological study of the meadows in Headquarter's Park, on the west slope of the Medicine Bow Mountains between 3048 and 3219 m elevation. His extensive data on species composition (60 species), soil moisture, and soil temperature serve to document the nature of the meadows as they exist now, so that future changes can be evaluated. Starr found that of the environmental factors he measured, only soil moisture was highly correlated with species composition. Snow release date did not appear to be a significant regulator of species composition in the meadows, though it did affect the time of flowering. All of his 50 stands were snow free within 14 days of each other, and most within 9 days. The latest observed snow cover on any stand in 1973 was July 5.

Starr (1974) classified the meadows of Headquarter's Park into 3 types:

1. Dry meadows, dominated by Sibbaldia procumbens, Potentilla

diversifolia, Viola adunca, and Polytrichum juniperinum.

II. Mesic meadows, dominated by Caltha leptosepala, Ranunculus alismaefolius, Carex illota,[1] and Deschampsia caespitosa.

III. Wet meadows (some bogs), dominated by Eleocharis pauciflora, Carex aquatilis, and mosses.

Tables 8, 9, and 10 summarize 3 years of above-ground biomass data for one stand of each meadow type in Headquarters Park (see Fig. 14 for meadow locations). Such data serve as another baseline against which future ecological changes can be judged.

The Dry Meadow at Headquarters Park had a total biomass of 97-159 g/m^2 on July 26, the minimum being during the driest year, 1972, and the maximum during the wettest year, 1973. Sibbaldia procumbens, Viola adunca, Carex illota,[1] and Agrostis thurberiana are most abundant and comprise two-thirds of the total biomass (Table 8). Erythronium grandiflorum and Claytonia lanceolata are common earlier, but have decomposed by late July. Sibbaldia procumbens comprised 38% of the total biomass in 1972, and since this species is considered to be well adapted to snow accumulation areas, the Dry Meadow may be quite tolerant of increased snowfall. Erythronium grandiflorum is also thought to be well adapted to snow accumulation. Starr (1974) estimated that roughly one-third of Headquarters Park is in the dry meadow type.

The Wet Meadow at Headquarters Park is very different, having water on the soil surface later into the growing season. At the end of July, 1972, the biomass per m^2 was 283 g, nearly 3 times the biomass on the Dry Meadow and the maximum biomass observed during the 3 years even though 1972 was the driest. Apparently summer precipitation is relatively unimportant for the wet meadows. Carex illota[1] is the most abundant species, followed by Deschampsia caespitosa and Caltha leptosepala (Table 9). Other common species included Juncus drummondii, Phleum alpinum, Ranunculus alismaefolius, and Trisetum woolfii.

The SCS Meadow is mesic and appears quite different from the other two meadows, though the total above-ground biomass is about the same as on the Wet Meadow. Biomass was measured in mid-July and mid-August, with no great difference in total biomass but a large shift in the

[1] Possibly Carex ebenea.

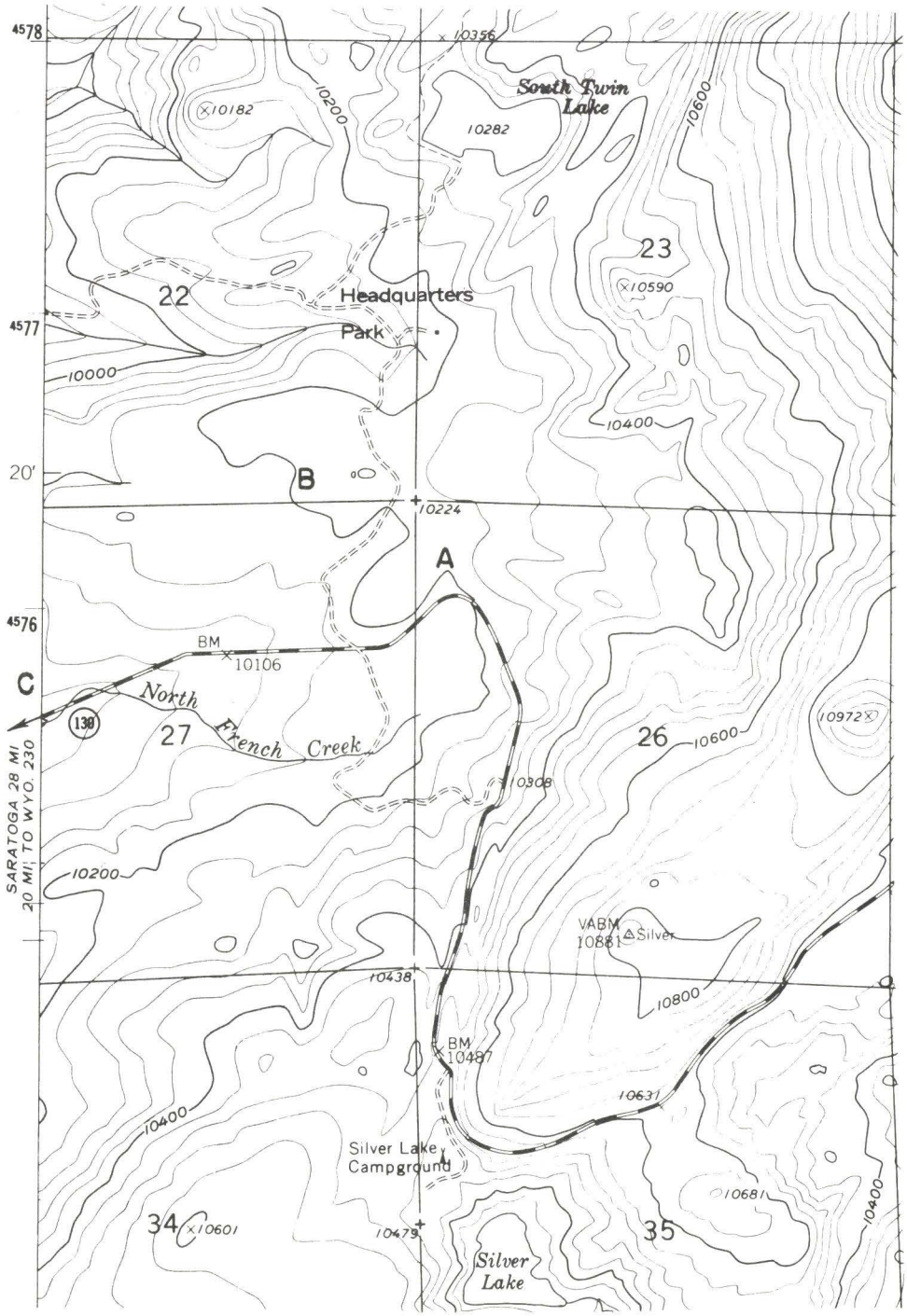

Fig. 14. Location of meadows sampled for above-ground biomass at Headquarters Park in 1972, 1973, and 1974. Dry Meadow (A), Mesic Meadow (C), and Wet Meadow (B).

TABLE 8. Above-ground biomass data (g/m^2, dry weight) for the dry meadow at Headquarters Park (Headquarter Park I) on July 26, 1972-74. Nomenclature follows Harrington (1954).[1]

Species	1972 g/m^2	1972 % Total Biomass	1973 g/m^2	1974 g/m^2
Achillea lanulosa	2	2.1		
Agrostis thurberiana	6	6.2		
Arenaria rubella	5	5.1		
Carex illota, possibly C. ebena	8	8.2		
Draba stenoloba	+	+		
Erigeron?	1	1.0		
Juncus drummondii	3	3.1		
Lewisia pygmaea	1	1.0		
Luzula spicata	1	1.0	Biomass was not sorted by species in 1973 and 1974.	
Phleum alpinum	1	1.0		
Plantago tweedii	2	2.1		
Poa alpina	1	1.0		
Poa reflexa	4	4.1		
Polygonum bistortoides	1	1.0		
Potentilla diversifolia	1	1.0		
Selaginella sp.	4	4.1		
Sibbaldia procumbens	37	38.1		
Stellaria borealis	1	1.0		
Thlaspi alpestri	+	+		
Veronica wormskjoldii	+	+		
Viola adunca	13	13.4		
Polytrichum juniperinum (moss)	5	5.2		
Veronica (gentian)?	+	+		
Viola-like unknown	+	+		
TOTAL	97 g/m^2		159 g/m^2	107 g/m^2

[1] See Appendix I for common names and authorities.

TABLE 9. Above-ground biomass data (g/m^2 dry weight) from the wet meadow at Headquarters Park on July 31, 1972-74.

Species	1972 g/m^2	1972 % Total Biomass	1973 g/m^2	1974 g/m^2
Agrostis thurberiana	2.0	0.6		
Arnica mollis	7.0	2.5		
Caltha leptosepala	34.0	12.0		
Carex aquatilis	1.0	0.3		
Carex illota, possibly C. ebena	87.0	30.7		
Deschampsia caespitosa	52.0	18.4		
Epilobium halleanum	2.0	0.6		
Erigeron peregrinus	7.0	2.5		
Juncus drummondii	10.0	3.5	Biomass was not sorted into species in 1973 and 1974.	
Juncus mertensiana	0.1	+		
Pedicularis groenlandica	1.0	0.3		
Phleum alpinum	11.0	3.9		
Poa reflexa	2.0	0.6		
Polygonum bistortoides	0.3	0.1		
Potentilla diversifolia	0.2	+		
Ranunculus alismaefolius	14.0	4.8		
Sedum rhodanthum	0.2	+		
Senecio dimorphophyllus	3.0	1.0		
Stellaria borealis	0.3	0.1		
Trisetum woolfii	12.0	4.0		
Trollius laxus	0.2	+		
Veronica wormskjoldii	0.8	2.8		
Unknown Moss #1	29.0	10.2		
Eleocharis pauciflora	8.0	2.8		
Gentiana sp.	0.1	+		
TOTALS	283		240	230

TABLE 10. Above-ground biomass data (g/m^2, dry weight) from the SCS Meadow (Headquarters Park II) on July 18 and August 15, 1972-74.

	JULY 18				AUGUST 15			
Species	1972 g/m^2	% Total Biomass	1973 g/m^2	1974 g/m^2	1972 g/m^2	% Total Biomass	1973 g/m^2	1974 g/m^2
Achillea lanulosa	3	1.0			1	0.3		
Agoseris glauca	3	1.0			4	1.3		
Agropyron trachycaulum					4	1.3		
Agrostis thurberiana					+	+		
Antennaria sp.	+	+			1	0.3		
Carex illota, C. ebenea?	44	15.4			107	35.9		
Carex sp.	4	1.4			1	0.3		
Carex sp.	+	+						
Claytonia lanceolata	1	0.4						
Deschampsia caespitosa	18	6.3			69	23.1		
Draba stenoloba	1	0.4			+	+		
Epilobium halleanum	3	1.0	Biomass was		1	0.3	Biomass was	
Erigeron sp.	2	0.7	not sorted		+	+	not sorted	
Erigeron sp.			by species		+	+	by species	
Erigeron peregrinus	10	3.5	in 1973-74.		28	9.4	in 1973-74.	
Erythronium grandiflorum	+	+						
Hordeum brachyantherum					3	1.0		
Juncus drummondii	11	3.8			1	0.3		
Lewisia pygmaea	1	0.4						
Phleum alpinum	11	3.8			10	3.3		
Plantago tweedii	44	15.4			32	10.7		
Poa annua	1	0.4			+	+		
Poa sp.	1	0.4			+	+		
Poa reflexa	13	4.6			9	3.0		
Polygonum bistortoides	16	5.6			8	2.7		
Potentilla diversifolia	5	1.7			8	2.7		
Ranunculus alismaefolius	65	22.8						
Rorippa curvipes?	1	0.4			3	1.0		
Senecio dimorphophyllus	12	4.2			3	1.0		
Sibbaldia procumbens	1	0.4			+	+		
Spergularia rubia	+	+			+	+		
Stellaria borealis	+	+			+	+		
Taraxacum officinale	5	1.7			1	0.3		
Thlaspi alpestre	+	+						
Trisetum spicatum	1	0.4			+	+		
Veronica sp.	+	+						
Veronica wormskjoldii	3	1.0			2	0.7		
Viola sp.	+	+			+	+		
Unknown grass	+	+						
Unknown grass	2	0.7						
Unknown grass	2	0.7						
Average g/m^2	285		213	240	298		345	232

contribution of several species. Carex illota and Deschampsia caespitosa were dominant at both times, but much more so in August (Table 9). Other less abundant species with this same trend are Erigeron peregrinus and Agoseris glauca. A larger number of species declined in biomass between mid-July and mid-August, in particular Ranunculus alismaefolius, Polygonum bistortoides, and Senecio dimorphophyllus. Plantago tweedii was about equally abundant both times.

Smith and Johnson (1965) investigated the biomass of three other subalpine meadows in the Medicine Bow Mountains. They found maximum standing crop to occur as early as July 1 and to consistently occur by late July. Maximum biomass ranged from 63.8 g/m^2 on the least productive site to 280 g/m^2 on the most productive site. At Headquarters Park the maximum biomass observed in a subalpine meadow was 345 g/m^2, on a wet site and during a wet year (1973).[1]

Alpine timberline in the Medicine Bow Mountains, as elsewhere, is not easily explained. Griggs (1938) and Daubenmire (1954) have reviewed the possible explanations and no summary is necessary here. Lindsay (1971) studied timberline in the Medicine Bow Mountains and concluded that water stress is a significant limiting factor to tree growth at high elevations. Snow is apparently of some importance in certain areas. Brink (1959) observed an advancing timberline and attributed this to less snowfall during the last century. A receding tree line with more snowfall cannot be assumed, of course, but Billings (1969) described a ribbon forest -- snow glade phenomenon near timberline in the Medicine Bow Mountains, illustrating that large snow drifts can break the continuity of subalpine forests. Either forest margins or existing "ribbon forests" function as snow fences causing the accumulation of snow in the forest or snow glade, as the case may be. If the snow drift in the forest persists until late summer, the trees may die; or in the case of the snow glade drift, seedlings do not become established. The snow glade on the east edge of Cinnibar Park in the Medicine Bow Mountains had snow until August 6 in 1972. Long persisting drifts either shorten the growing season below a certain threshold, or create soil conditions that are intolerable to the seedlings. Brown-felt fungi are also very

[1] See Appendix III for plant biomass data collected on tundra and meadow sites near Medicine Bow Peak.

frequent on seedlings that do occur occasionally in the snow glade.

The Snowy Range area of the Medicine Bow Mountains has been the site of many studies on alpine ecology, some of which seem quite relevant to precipitation management. For the purposes of our project, we consider the 3,333 m (11,000 ft) contour as the approximate lower limits of the alpine zone in the Medicine Bow Mountains. The true alpine zone covers an area of about 16 to 18 km^2.

Vegetation in the alpine zone is quite variable, and many ecologists consider a vegetation classification based on only species composition to be extremely arbitrary. Classifications based on the physiognomy of the vegetation and site factors can be more easily constructed, for example the following:

I. Willow (Salix planifolia) thickets, along stream courses and in areas of deep winter snow cover.

II. Sedge bogs (Carex and Juncus spp.), found along the edge of lakes and ponds, and in areas advanced in hydrarch succession.

III. Wet meadows, found in areas slightly less moist than the sedge bogs, such as below long-lying snowbanks which contribute water during the growing season. Tufted hairgrass (Deschampsia caespitosa) is particularly common.

IV. Dry meadows, found on drier sites. Tufted hairgrass and alpine bluegrasses (Poa spp.) are the dominants. The Kobresia meadow community common in the alpine zone of Colorado does not occur in the Medicine Bow Range.

V. Forb turf, present on dry sites. The most common taxa are alpine avens (Geum rossii), alpine clover (Trifolium spp.), alpine sagewort (Artemisia scopulorum), and bistort (Polygonum bistortoides).

VI. Arid tundra, a community found on the driest sites, especially windswept areas, and with most plants having the cushion growth form. Many species are present but phlox (Phlox spp.), alpine clover, and moss campion (Silene spp.) are common.

In general the alpine zone is a dry area for plant growth, in spite of the fact that it receives considerable precipitation (24-29 inches or 600-740 mm in the Medicine Bow Mountains). Most of the precipitation

is in the form of snow and the soil is usually frozen for long periods. This, combined with the extremely windy conditions (40-50 km/hr winds are generally constant through the winter period) leads to considerable plant moisture stress during much of the year. These factors, combined with low temperatures, tend to limit plant growth.

While the alpine zone of the Medicine Bow Mountains is not extensive, it has been intensively studied, primarily by Billings and his students. Bliss (1956) studied the relationship between alpine plant growth, as measured by stem elongation and leaf expansion, and the following environmental factors: (1) solar radiation, (2) air, surface and soil temperatures, (3) precipitation, (4) vapor pressure deficit, (5) wind, and (6) soil moisture. He found only low correlations between air and soil temperatures and stem elongation. Standing crop ranged from 26.7 g/m^2 at the most exposed xeric site to 112.4 g/m^2 at a wet meadow site.

Billings and Bliss (1959) made a 2-year (1954 and 1955) study of the vegetation associated with a single snowbank in the Snowy Range section of the Medicine Bow Mountains. They sampled two locations -- above and below the snowbank -- at weekly intervals. Maximum total above-ground standing crop on the upper area varied from 27.0 g/m^2 to 57.8 g/m^2 and usually occurred 3 to 4 weeks after snowmelt. On the lower site the range was 21.3 g/m^2 to 141.3 g/m^2 which occurred three to five weeks after snowmelt. Average daily productivity was 2.8 g/m^2/ day on the upper site and 6.0 g/m^2 on the lower site. Often the maximum productivity was recorded immediately after snowmelt. Little difference was found in air temperature or vapor pressure deficit between the upper and lower sites and the difference in plant productivity was thought to be the result of the amount of available soil moisture and the length of time the plants were released from snow cover. Our research also found an effect of snow duration on species composition (p. 175).

Scott (1963) made a detailed study of the relationships between standing crop, primary productivity and environmental factors in the alpine region of the Medicine Bow Mountains. He found above-ground standing crop to vary from 14 to 348 g/m^2, with most sites (29

of 50) between 100 and 200 g/m^2. His statistical analysis indicated the following were important environmental variables: (1) altitude, (2) estimated winter snow cover, (3) estimated moisture regime, (4) estimated soil movement, (5) extractable K, (6) available water in the subsoil. Factors 2, 3, 4, and 6 could be affected by winter precipitation management.

With regard to primary productivity, Scott estimated 11.1 g/m^2/day for a mesic site and 1.2 g/m^2/day on a xeric site, both estimates being average values for a 6-week period in June and July 1962. Weekly total productivity on the mesic site was correlated with: (1) weekly solar radiation, (2) weekly air flow, (3) soil temperature and (4) soil moisture. Only solar radiation was correlated with weekly total productivity on the xeric site and this was significant only at the 10% level. Scott attributed this lack of correlation "to the low accuracy of the xeric station data", masking any correlation with environmental factors.

Smith (1969a) measured the above-ground standing crop on 29 sites at or above timberline in the Medicine Bow Mountains. The average above-ground standing crop was 60.3 g/m^2 with a range of 7.8 to 115.7 g/m^2. Two species, Deschampsia caespitosa and Geum rossii, produced 23% of the herbage sampled. Production of herbage was found to be most significantly related to the silt and clay content and pH of the A horizon, and slightly less significantly related to the organic matter content of the A horizon and the extractable potassium in the solum. Geum rossii was most common on coarse textured soils of high organic content and Deschampsia caespitosa tended to occur on the more finely textured soils of relatively low organic content. Smith also indicated the moisture content of the soil influenced the distribution of these two species, basing his assumption on the presence of gley horizons and the degree of mottling, both of which tend to indicate wet soils. Deschampsia caespitosa was more prevalent but not confined to soils with the "wet" characteristics.

Thilenius, et al (1974), in a study of the effect of 2,4-D on composition and production of an alpine community dominated by

Trifolium parryi, Geum rossii and Artemisia scopulorum, found total standing crop on untreated areas to average 135 g/m^2 with a range of 119 g/m^2 to 155 g/m^2 over a 4-year period. The three major species produced half of the total standing crop. Application of 2,4-D did not affect total standing crop, which averaged 127 g/m^2 with a range of 108 g/m^2 to 142 g/m^2 on sprayed areas over the same period. Species composition on the sprayed area was significantly altered from a forb-dominated vegetation to a vegetation dominated by grasses (Deschampsia caespitosa and Poa rupicola).

An apparent frost hummock-sorted polygon cycle was described by Billings and Mooney (1959) in the Libby Flats area. Their results indicate that wind erosion and frost thrusting can cause degradation of mature peat hummocks through frost scars to sorted polygons (frost boils).

Mooney and Billings (1960, 1961) studied the carbohydrate cycle of three alpine species (Saxifraga rhomboidea, Polygonum bistortoides and Geum rossii) from the beginning of one growing season until the start of the following one. Growth of these plants was found to be very rapid, commencing in some instances under a cover of snow. The underground organs contained relatively large amounts of carbohydrate reserves, a large proportion of which is utilized in growth prior to snowmelt and during the period of rapid shoot growth immediately following snowmelt. In Polygonum, 50% of the rhizome reserves were used in a one week period during early growth. Except for this short period of rapid depletion in rhizomes and roots during early growth, high carbohydrate levels were maintained both in the shoot and in the underground organs during most of the growing season. Generally, the lowest carbohydrate reserve level in both root and shoot occurred before flowering, a relatively high level was maintained in the shoot from flowering until after fruiting, while peak storage in underground parts was reached at the start of fall dormancy. The carbohydrate cycle in these alpine plants is quite similar to that in certain arctic plants, and appears to be adaptive for short-growing seasons.

In a later paper Mooney and Billings (1965) studied the effects of altitude on the carbohydrate content of several species. Carbohydrate reserves were higher near the lower altitudinal limits of several species they studied. The higher carbohydrate content of individuals in natural populations near the lower altitudinal limits of an alpine species appeared to be an adaptation for the warmer environment where metabolism may occur more rapidly.

Field measurements of photosynthesis and respiration rates of whole alpine plants in situ were made at an elevation of 3,307 m in the Medicine Bow Mountains, Wyoming, using an infrared gas analyzer (Billings et al 1961). Maximum net photosynthesis rates ranged from 4.15 to 13.4 mg CO_2/dm^2 two surfaces/hr with an average rate of 9.32. An all-day measurement on Geum rossii during somewhat cloudy weather showed net photosynthesis paralleling and responding to changes in light and temperature. Similar measurements of Polygonum bistortoides in clear sunny weather showed a midday depression in net photosynthesis, due perhaps to high leaf temperatures under intense solar radiation. Net photosynthesis of whole sod blocks averaged 6.23 mg CO_2/g dry wt/hr. Soil CO_2 output averaged 1.846 mg CO_2m^2/hr which they report as higher than published results from lower altitudes. Rough estimates of dry weight gain as calculated from sod-block metabolic rates average 2.79 g dry wt/m^2/day.

Water content of alpine plants in the Medicine Bow Mountains was studied by Hill (1964) to determine the water relationships between these plants and their environment, where climatic conditions are characteristically severe. Hill found that although soil moisture probably did not limit rates of absorption, atmospheric factors determining transpiration rates were severe. These plants demonstrated a remarkable capacity to tolerate large diurnal variations of water content without apparent wilt. The plants' adaptations to the severity of the alpine environment are reflected in this ability to withstand large fluctuations in water content.

In summary, there is a rather large body of information on the vegetation that is relevant to precipitation management. Specifically,

whatever can be learned about water relations, carbohydrate balance, and limiting factors will lead to more confident predictions on the possible effect, if any, of more snow. Our observations, and those of others, indicate that snow does affect plant species composition and productivity. We have observed situations in the Medicine Bow Mountains where aspen, pine, spruce, fir, and other plants could not survive, apparently due to snow accumulation; and other situations where some plants apparently survived because of considerable snow accumulation. The question is, will winter precipitation management modify existing snow accumulation patterns sufficiently to affect vegetation patterns? This question is considered further beginning on page 175.

Plant Production of Three High-Elevation Ecosystems

John F. Thilenius

The purpose of this study, conducted in 1972 and 1973, was to obtain additional baseline production data on 3 permanently located plots in the area where cloud-seeding might someday be effective in the Medicine Bow Mountains. The results are unique from other similar data presented on previous pages because roots are considered as well as above-ground biomass (shoots) and because the vegetation was sampled more intensively and more frequently.

Three study sites were located in the alpine-subalpine region (+3200 m elevation), Table 5. The environmental characteristics of each site are summarized beginning on page 23.

The Libby Flats Site (Fig. 15) is located at approximately 3230 m on a gentle (3-6%) north-facing slope, and could be reached by automobile after snowmelt. The vegetation is alpine turf.

The Lake Marie Site (Fig. 15) is located between 3450 to 3475 m. Exposure is west and slope angles are from 16% on the lower portion of the area to 10% above. The site is dissected with numerous stone stripes and boulder fields; sampling was done on alpine turf interspersed between these rocky areas. The site is accessible only by foot or horseback during the summer since it was located in an area prohibited to motorized vehicles during the snow-free period. It can be reached by over-snow vehicles when sufficient snow exists.

The Fourlog Park Site (Fig. 15) is located at about 3140 m, on a gentle (3-4%) east-facing slope. The site is surrounded on three sides by subalpine forest. Scattered pine and spruce were present in the area, but none were included in the sample. The vegetation is a subalpine mesic meadow of considerably different species composition than

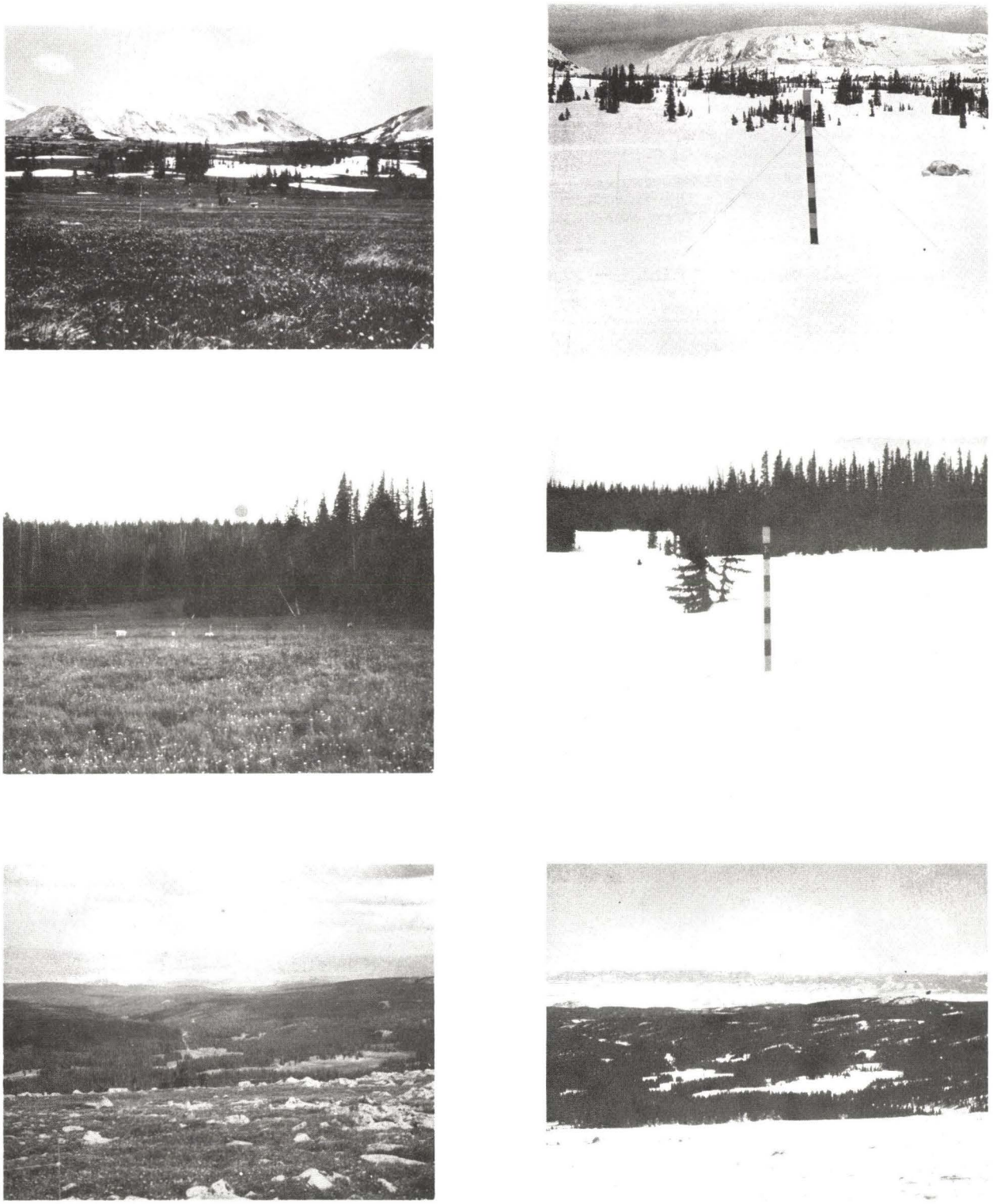

Fig. 15. Photos of the Libby Flats site (top), Fourlog Park site (middle), and Lake Marie site (bottom) in summer and winter.

the two alpine sites. A well-developed cryptogam stratum was not present and a considerable amount of bare soil was exposed by burrowing rodents.

Sampling Procedure

Five sample units were located on each site, each unit consisting of a randomly-located 5 x 14 m plot. Within each unit, two 1 x 12 m areas were reserved for sampling. These areas were separated by a 1 m wide interval to avoid trampling. Each of the two sample areas within the units was subdivided into 120, 20 x 50 cm quadrats (0.1 m^2) for a total of 240 quadrats/sample unit. The units were protected from livestock grazing by a two-strand electric fence.

The intimate association and small size of the plants to be sampled and the harsh alpine environment (strong winds, cold temperatures) made the determination of biomass by field harvesting of quadrats a very imprecise and difficult procedure. Consequently, all biomass samples were collected by removing a 65 mm diameter cylindrical core of soil, root material, litter and above-ground vegetation. A coring device was developed for this purpose. The technique was to insert the corer until a rock was hit. No attempt was made to go deeper. Cores as long as 50 cm were extracted. Examination of the cores indicated that most of the root biomass was concentrated in the upper 20 cm of the soil profile.

Immediately after removal the cores were enclosed in a capped plastic cylinder to facilitate transfer and storage and to minimize drying. The cores were stored at -22°C. The biomass sample consisted of 125 cores from each site at bi-weekly intervals. The cores were taken in groups of five randomly located 0.1 m quadrats in each of the five sample units at each site. In the laboratory the samples were handled as follows:

1. Thaw the core (if necessary).
2. Remove the above-ground vegetation; sort it to taxa separating live (green) and dead (brown or weathered) plant material; oven-dry at 105°C and weigh each taxon (total dead) to obtain

a measure of above-ground biomass by taxon. Ash the material in a muffle furnace at 900°C and reweigh to correct for any incorporated inorganic matter.

3. Remove the litter layer, oven-dry, weigh, ash in a muffle furnace, and reweigh to correct for any incorporated inorganic material.
4. Manually break up the soil-root cylinder to facilitate water penetration; place this broken-up material in a root washing machine; wash until the soil was removed (ca 20-30 min); oven-dry the root material; weigh to obtain a measure of below-ground biomass; ash in a muffle furnace and reweigh to correct for inorganic material. No attempt was made to identify the root material to taxon.

In 1972 biomass was measured five times at Libby Flats and Lake Marie and four times at Fourlog Park between late-June and late-August. In 1973 six biomass samples were obtained at Libby Flats and five at each of the other two sites. In all instances the absence of an early season sample was due to snow cover on the sites.

Above-Ground Biomass

The two alpine turf sites (Libby Flats and Lake Marie) were dominated by forbs, Geum rossii (GERO)[1] having the largest biomass at both sites. At Libby Flats, G. rossii produced an average of 37.2% of the live above-ground biomass in 1972 and 38.4% in 1973, and at Lake Marie it was even more dominant. The two yearly averages are very close at both sites.

Although over 50 species were recorded (Appendix III), only a few produced most of the biomass. Taxa producing more than 10% of the above-ground live biomass at least once during the 1972 and 1973 seasons on the two alpine sites were Artemisia scopulorum (ARSC), Selaginela densa (SEDE), Carex albo-nigra (CAAL), Polygonum bistortoides (POBI), Trifolium parryi (TRPA) and Deschampsia caespitosa (DECA). Concentration of the majority of the biomass in a few taxa is normal in alpine communities (Scott 1963).

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[1] Four-letter symbols for plant names are composed of the first 2 letters of the genus and species, respectively. See Appendix II for a list of species abbreviations and species authorities.

Table 11. Mean standing crop (g/m^2) for 1972 and 1973. See Appendix III also.

Sampling site		Sampling date										
		1972					1973					
		6/26	7/10	7/24	8/07	8/21	6/20	7/04	7/18	8/01	8/15	8/29
Libby Flats	Standing live	108.9	93.8	75.6	95.0	91.5	72.8	180.1	162.6	139.7	97.3	43.0
	Standing dead	70.4	122.9	148.8	270.6	423.0	143.1	208.5	159.3	229.8	161.2	90.1
	Vegetation	179.3	216.3	224.4	365.6	514.5	215.9	388.6	321.9	369.5	258.5	133.1
	Litter	251.1	303.6	189.6	73.3	88.0	408.6	269.1	115.5	213.2	140.9	178.8
	Above ground	609.7	737.0	414.0	438.9	602.5	624.5	657.7	437.4	582.7	399.4	384.7
	Below ground	3376.8	4641.8	4599.6	4452.4	3919.2	4174.1	4333.0	5755.8	3999.9	5821.7	5014.9
	Total	3986.5	5378.8	5013.6	4891.3	4521.7	4798.6	4990.7	6193.2	4582.6	6221.1	5399.6
		6/27	7/11	7/25	8/08	8/22	6/21	7/05	7/19	8/02	8/16	8/30
Lake Marie	Standing live	55.3	71.6	77.4	109.9	143.5	NS[1/]	61.2	97.3	114.8	72.5	67.4
	Standing dead	84.6	84.5	124.9	139.6	468.2		281.4	349.9	284.8	74.4	74.6
	Vegetation	139.9	156.1	202.3	249.5	611.7		342.6	447.2	399.6	146.9	142.0
	Litter	173.2	205.8	180.5	214.0	72.8		114.7	121.8	192.6	181.7	81.0
	Above ground	313.1	361.9	382.8	463.5	684.5		457.3	569.0	592.2	328.6	223.0
	Below ground	3973.1	4482.2	4239.2	6354.1	4391.7		4443.8	4299.9	5212.2	6631.1	7186.4
	Total	4286.2	4844.1	4622.0	6817.6	5076.2		4901.1	4868.9	5804.4	6959.7	7409.4
		6/28	7/12	7/26	8/09	8/23	6/22	7/06	7/20	8/03	8/17	8/31
Fourlog Park	Standing live	NS	55.2	70.6	67.7	73.5	NS	72.9	144.8	126.0	111.8	88.6
	Standing dead		62.8	119.9	102.2	153.3		119.3	199.1	180.6	88.1	84.8
	Vegetation		118.0	190.5	169.9	226.8		191.2	343.9	306.6	199.9	173.4
	Litter		325.9	113.0	124.1	34.7		163.6	108.2	96.3	209.0	146.1
	Above ground		443.9	303.5	294.0	261.5		354.8	452.1	402.9	408.9	319.5
	Below ground		2737.9	3031.7	3204.6	2729.6		2981.4	3400.5	3093.8	2874.5	3025.7
	Total		3181.8	3335.2	3498.6	2991.1		3336.2	3852.6	3496.7	3283.4	3345.2

[1/] NS: No sample taken because of snow cover on sampling site.

Overall, species composition on the two alpine sites was similar with Geum rossii the dominant taxon and Artemisia scopulorum the major sub-dominant. The major qualitative difference in composition was the presence of Sibbaldia procumbens (SIPR) at Lake Marie and not at Libby Flats. Sibbaldia procumbens is a species characteristic of snow accumulation areas throughout the northern hemisphere (Willard and Harris 1971) and its presence at Lake Marie is indicative of the greater snow accumulation on that site.

Conversely, Trifolium parryi was more abundant at Libby Flats than at Lake Marie; on Libby Flats it ranked fourth in productivity in 1972 and third in 1973.

The most productive species at Fourlog Park was Carex ebenea[1] (CAEB) which produced an average of 28.4% of the above-ground live biomass in 1972 and 19.5% in 1973. Carex ebenea[1] is present at both the alpine sites but only as a minor component of the vegetation. The same is true of the third-ranked taxon, Potentilla diversifolia.

While Carex ebenea[1] was the most productive, it did not have the clear-cut dominance of Geum rossii at the alpine sites. Other species producing from 14 to 20% of the above-ground live biomass in 1973 were Potentilla diversifolia (PODI), Erigeron simplex (ERSI), Lewisia pygmaea (LEPY), Poa cusickii (POCU), Sibbaldia procumbens (SIPR), and Stipa lettermannii (STLE). In 1972, Deschampsia caespitosa (DECA) and Stipa columbiana (STCO) were the most productive subordinant taxa, along with Potentilla diversifolia.

The two species of needlegrass (Stipa columbiana and S. lettermannii) were present only at Fourlog Park. They grew sympatrically and together outproduced the dominant Carex ebenea[1]. In 1972 Stipa lettermannii was more productive earlier in the growing season than Stipa columbiana and in 1973 it was more productive throughout the whole season. Poa cusickii (POCU), P. rupicola (PORU), and P. alpina (POAL) were also abundant at Fourlog Park.

The within-year distribution of above-ground live biomass was very different in 1972 and 1973 (Fig. 16). In 1972 the greatest above-ground

[1] Possibly Carex illota.

live biomass at Libby Flats was recorded at the first sampling date. There was a decline in this parameter until the third sampling date, and then a slight increase occurred. Both Lake Marie and Fourlog Park showed steady season-long increases, with Lake Marie having the greater and Fourlog Park showing only a very slight increase.

In 1973 all sites showed bell shaped or skewed growth curves. Peak values were earliest at Libby Flats, second at Fourlog Park and last at Lake Marie, where the largest biomass was measured 28 days later than at Libby Flats. The 1973 samples were taken seven days earlier than those in 1972. If the earliest sample date at Libby Flats in 1973 is ignored the growth curve has generally the same downward trend as it had in 1972, albeit the absolute amount of above-ground live biomass at Libby Flats is much greater in 1973 than in 1972. Possibly, the period of greatest increase was missed at Libby Flats in 1972, though 1972 was also much drier.

The seasonal trends in litter and standing dead biomass are shown in Fig. 17.

Below-Ground Biomass

To incorporate the depth dimension and yet retain the area-based comparison, below-ground biomass is reported as g/m^2 to the average depth of the core sample in the following manner: 7186 g/m^2:19.9 cm, which on a volume basis would be 7186 g/0.199 m^3.

While the estimates for above-ground biomass fell within the observed range for high elevation ecosystems in the Medicine Bow Mountains (Scott 1963, Bliss 1956, Billings and Bliss 1959, Smith and Johnson 1965, Thilenius et al 1974), the estimates of below-ground biomass far exceed any of the reported values. Yearly averages were:

	1972	1973
Libby Flats	4198 g/m^2:13.2 cm	4850 g/m^2:15.6 cm
Lake Marie	4688 g/m^2:18.3 cm	5555 g/m^2:21.5 cm
Fourlog Park	2926 g/m^2:13.7 cm	3075 g/m^2:16.5 cm

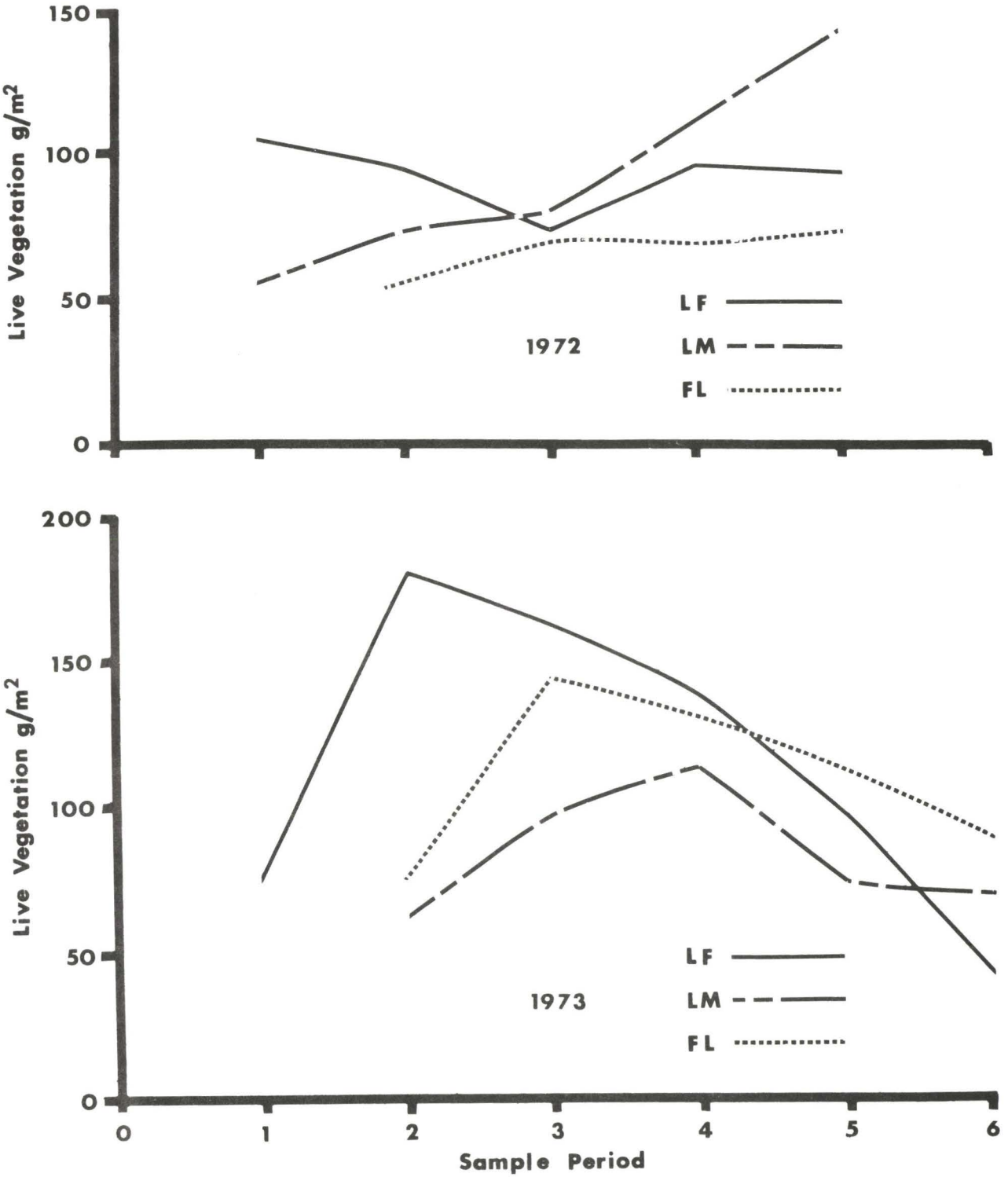

Fig. 16. Seasonal changes in living above-ground plant biomass during 1972 and 1973 at Libby Flats (LF), Lake Marie (LM), and Fourlog Park (FL). Samples were taken at 2 week intervals beginning on June 27 and June 20 in 1972 and 1973, respectively. See Table 11 for exact dates.

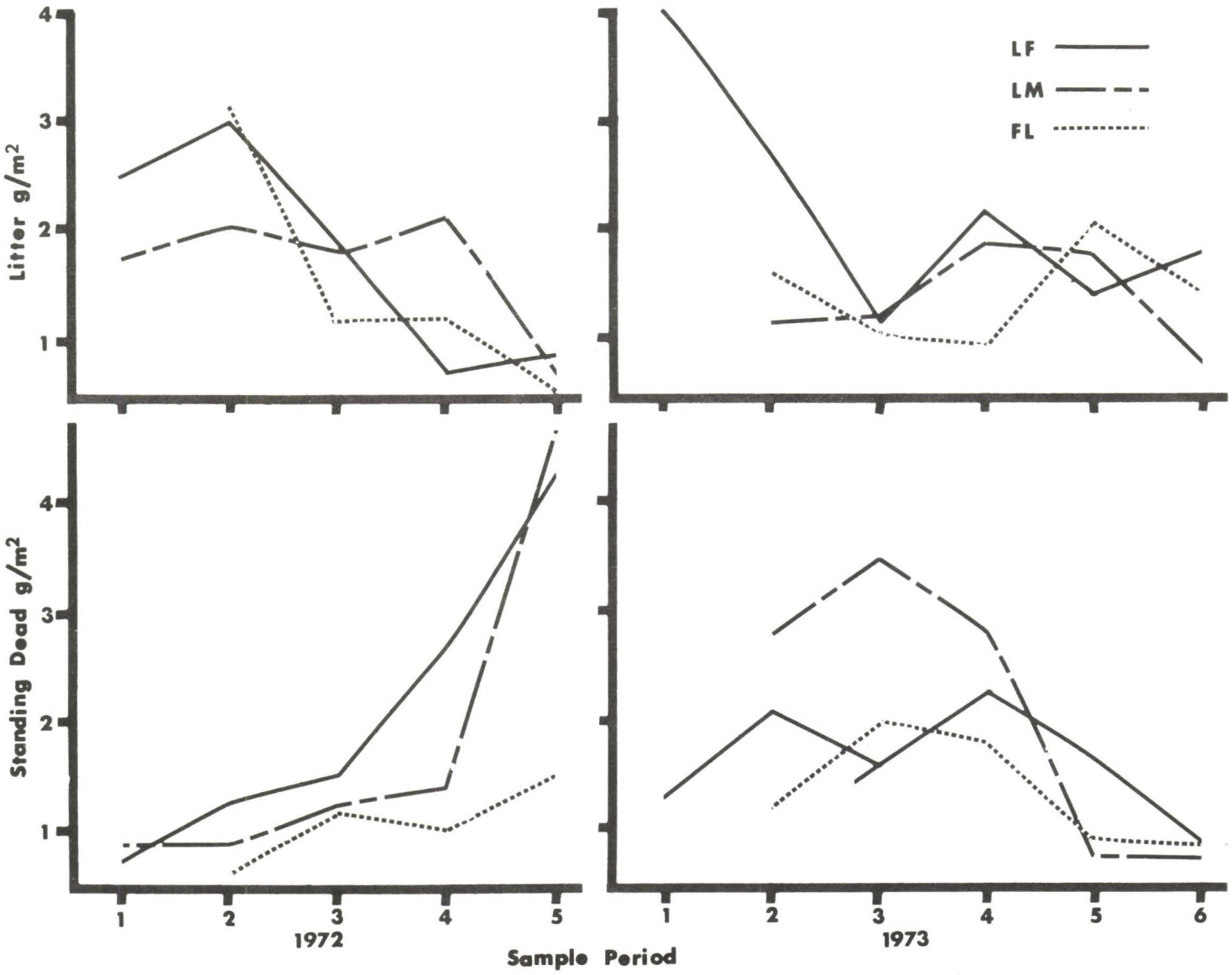

Fig. 17. Seasonal changes in litter and standing dead biomass during 1972 and 1973 at Libby Flats (LF), Lake Marie (LM), and Fourlog Park (FL). Sample dates were the same as described in Fig. 16 and Table 11.

The standard error of the means for these averages are low (Table 12), the highest being 7.1 percent of the average. Most were in the range of 3 to 5 percent of the average. Thus, the values appear to be accurate estimates of the below-ground biomass on the three sites.

Bliss (1963) reported the underground biomass of an alpine mesic sedge meadow on Mt. Washington, New Hampshire, as 3634 g/m^2, and Scott (1963) gave the underground biomass of an alpine mesic turf site in the Medicine Bow Mountains as 1400 g/m^2, and that of the xeric site as 750 g/m^2. The depth to which root biomass was determined is not given.

The highest yearly averages and the highest single value were recorded at Lake Marie. In late August 1973, a value of 7186 g/m^2: 19.5 cm was obtained. This is about twice the maximum value reported by Bliss (1963) and over five times that reported by Scott (1963). The highest value at Libby Flats was 6354 g/m^2:19.9 cm in early August 1972. At Fourlog Park, the maximum value of 3401 g/m^2: 19.2 cm was measured in late July 1973. Below-ground standing crop was greater on all sites in 1973. Libby Flats and Lake Marie had proportionally greater increases in 1973 (ca 650-870 g/m^2) than did Fourlog Park.

There was little uniformity between sites in the seasonal trend of below-ground biomass (Fig. 18). Part of this can be due to sampling error caused by within-site variations in soil depth. During the core sampling it became apparent that it was not possible to predict depth of core from the surface vegetation. Cores extracted from sites with little or no surface vegetation could be either shallow or deep as could cores with abundant surface vegetation. On an average, core depths were greatest at Lake Marie (ca 19.9 cm) and almost equal in depth at Fourlog Park (ca 14.7 cm) and Libby Flats (ca 14.4 cm). The almost 5 cm greater average depth at Lake Marie may account for the greater below-ground biomass at this site. However, the below-ground biomass at Libby Flats greatly exceeded that at Fourlog Park although the soil depths at both sites were about equal. The difference here is most likely due to the difference in how plants are adapted to an alpine turf ecosystem and a subalpine meadow ecosystem.

Table 12. Average core depth (cm) and average below-ground standing crop (g/m^2)

Sample site	Sample date	Core depth $\bar{X}$	± $S_{\bar{x}}$	Standing crop $\bar{X}$	± $S_{\bar{x}}$
Libby Flats					
1972	6/26	12.5	0.5	3377	120
	7/10	14.3	0.5	4642	160
	7/24	13.2	0.6	4600	170
	8/07	13.3	0.4	4452	180
	8/21	12.7	0.5	3919	150
1973	6/20	18.9	0.7	4174	130
	7/04	16.6	0.6	4333	160
	7/18	15.5	0.6	5756	400
	8/01	16.1	0.5	3999	190
	8/15	14.6	0.5	5821	170
	8/29	12.0	0.4	5015	230
Lake Marie					
1972	6/27	17.3	0.7	3973	170
	7/11	18.4	1.0	4482	200
	7/25	19.5	1.0	4239	280
	8/08	19.9	0.9	6354	310
	8/22	16.3	0.9	4392	230
1973	7/05	21.8	0.8	4444	180
	7/19	25.5	0.9	4300	160
	8/02	21.0	0.8	5212	210
	8/16	20.6	0.7	6631	470
	8/30	19.5	0.8	7186	490
Fourlog Park					
1972	7/12	15.9	0.7	2738	130
	7/26	13.4	0.6	3032	180
	8/09	12.9	0.5	3204	180
	8/23	12.6	0.5	2730	110
1973	7/06	19.3	0.7	2981	110
	7/20	19.2	0.8	3401	210
	8/03	17.8	0.7	3094	120
	8/17	12.8	0.5	2875	130
	8/30	13.6	0.6	3025	110

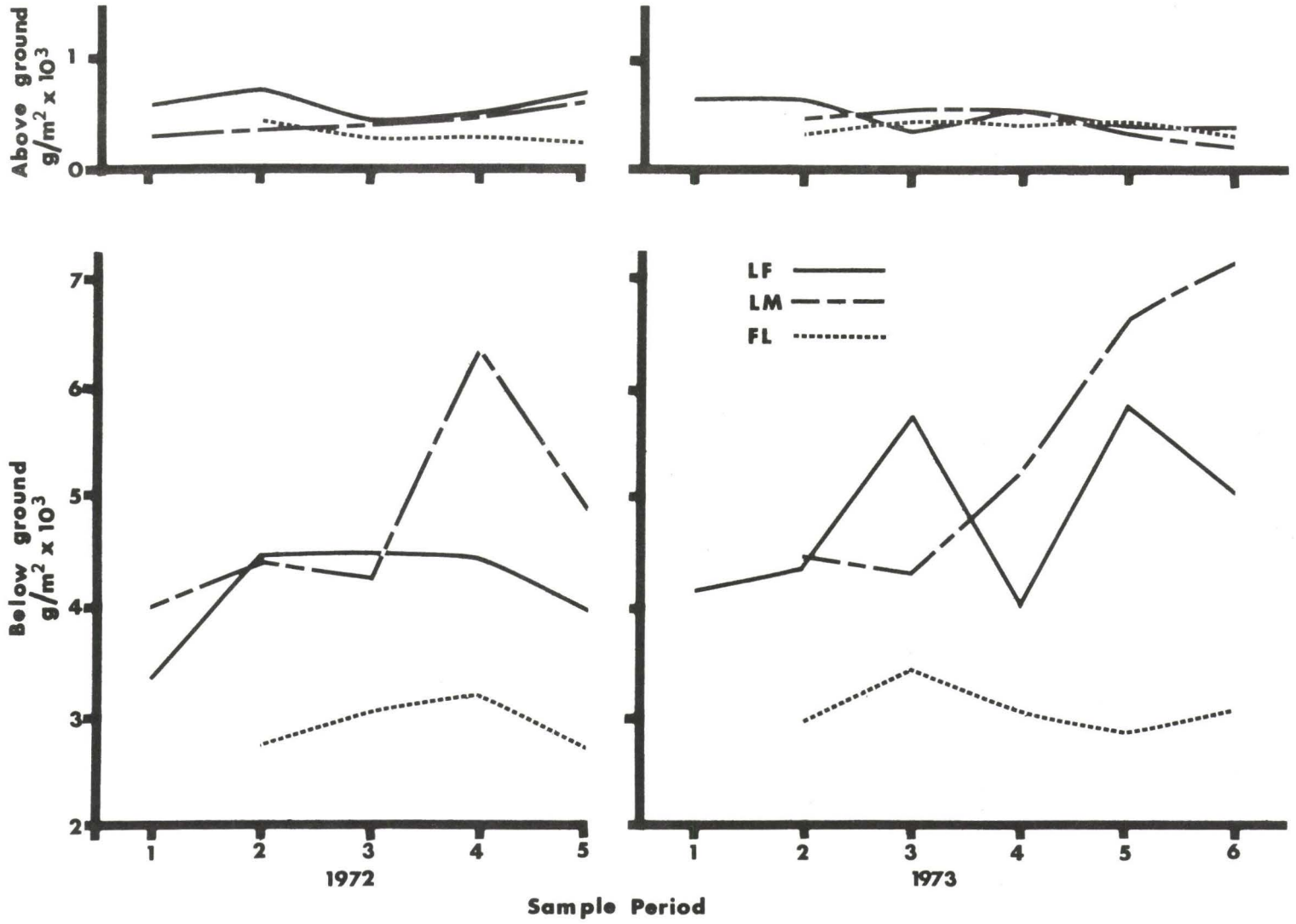

Fig. 18. Seasonal changes in total above-ground and below-ground biomass in 1972 and 1973 at Libby Flats (LF), Lake Marie (LM), and Fourlog Park (FL). Sample dates were the same as described in Fig. 16 and Table 11.

Strong relationships between total above-ground biomass and total below-ground biomass were not evident (Fig. 18). At Libby Flats in 1972 both above- and below-ground biomass increased from late June to early July and there is no evidence of a decrease in below-ground biomass associated with the transfer of material from roots to the above-ground portion of the vegetation. This was true both for the live biomass as well as total above-ground biomass. The large increase in below-ground biomass at Lake Marie in early August was not accompanied by any decrease in above-ground biomass. In fact, above-ground biomass was higher at this time than it was at the previous sample date.

In 1973 a weak inverse relationship between above- and below-ground biomass was present at Libby Flats. The peaks of below-ground biomass were accompanied by corresponding declines in above-ground biomass or vice versa. However, this did not occur at either Lake Marie or Fourlog Park.

As can be seen in Fig. 18, most of the producer biomass of alpine ecosystems is below ground. Scott (1963) observed a ratio of above- to below-ground biomass (A:B ratio) of 20:80, i.e. 80 percent of the producer biomass is below ground (Scott 1963). In the two alpine ecosystems sampled in this study the A:B ratio is between 15:85 and 3:97 with averages for Libby Flats of 12:88 in 1972 and 10:90 in 1973. Corresponding averages for Lake Marie are 8:92 in both 1972 and 1973. A:B ratios are not available from other studies for subalpine grassland sites such as Fourlog Park. The average values determined in this study are 10:90 in 1972 and 11:89 in 1973.

Because the values for below-ground biomass reported here are much higher than those in the literature, it is appropriate to indicate that the difference is probably due to different technique. Scott (1963) washed an average of 20 plants of individual species and then dried, separated, and weighed these individuals. His values are summations of individual species. The below-ground biomass estimates in my study were obtained by washing the soil from individual cores and are not species summations. Bliss (1956) indicated that he washed his below-ground biomass samples using a 2 mm sieve. I used sieves of 0.42 mm

and 0.25 mm mesh. A normal 20-minute washing of 20 cores would fill the 0.25 mm mesh sieve (20 cm diameter by 5 cm) to capacity with material which had already passed through a 0.42 mm sieve. Most of this material was organic since it was almost all burned when placed in a muffle furnace. Thus, the high values for below-ground biomass reported here may be partly due to improved washing techniques.

Discussion

Change in an ecological attribute such as biomass means a significant difference (either in a statistical or some other sense) from what has been established as the normal level or value of that attribute. Measurements of the amount and direction of the change is in itself a problem, particularly in natural situations where the usual technique of control and treatment may be difficult if not impossible to establish. Consequently, the more common practice is to determine pretreatment levels or values of attributes and establish a baseline from which changes can be measured.

The establishment of baseline levels is not as simple as it may appear. For example, Fig. 16 shows the seasonal fluctuation in the total above-ground biomass of live vegetation at the three sites in the Snowy Range for two growing seasons. The curves representing the changes in total biomass of live vegetation are not at all comparable between sites, years, or sites within years. Even a single parameter such as the time and amount of maximum biomass of live vegetation was variable between years. While season-long averages can (and were) calculated for each site in each year, these averages represent quite different growth patterns. Those for 1972 are the average of generally concave to straight-line curves, while in 1973 the curves are convex. Thus, even if identical averages were obtained (which did not occur in this study) they would represent a very different production sequence.

The fluctuations in the timing and amount of the above-ground biomass of live vegetation also indicates the usual method of estimating the parameter with a single growing season measurement at the "time of

maximum development" is inadequate. Samples must be taken at relatively short intervals throughout the growing season if an accurate estimate is to be made. Furthermore, this determination must be made over a period of several years to determine if there is a defined pattern of growth and should be combined with concurrent measurements of the phytomicroclimate. Measurements should also be made at a number of geographic locations (sites). As shown, even two alpine sites with similar composition had quite different growth patterns.

From the above, it can be seen that the determination of a "baseline value" is not an easy task. It requires considerable manpower and financial support over a period of time longer than 2 years.

It is perhaps appropriate to point out some of the things learned in this study with regard to sampling techniques. For high elevation ecosystems, with their harsh environment, the extraction of cores from which the standing crop can be determined seems to have several advantages. First, it allows all subdivisions of biomass (above-ground live, standing dead, litter, and below-ground) to be determined. Secondly, these determinations can be done in the relative comfort of the laboratory, which increases accuracy. Third, while the technique is destructive -- as are all sampling techniques for weight determinations to some extent -- its impact on the sampled site is not extreme. The old core holes are difficult to see except from directly above, even in low alpine vegetation, and one year after sampling the holes had begun to fill. Finally, an adequate sample can be taken in a relative short time. In this study, two men could extract 125 cores in about 4 hours working time without undue fatigue. Transportation of the extracted cores from remote sites is a problem since they are heavy.

As described earlier, various environmental factors were monitored at the 3 sites during 1972 and 1973 (see p. 23). It has not yet been possible to study in detail the relationships between the various factors and species productivity, but some observations are noteworthy.

First, the growing season of 1973 was noticeably wetter and this was the year with the largest amount of biomass, both above ground and below (Figs. 16 and 18). The larger root production occurred in 1973,

even though the average soil temperatures below 5 cm were cooler that year. The data suggest that either summer rainfall or lower saturation deficit is favorable to primary productivity at these high elevation sites.

Secondly, as noted the biomass curves for 1972 and 1973 are quite different in shape, being bell-shaped in 1973 and linear or convex in 1972. Since the bell-shaped curves might be expected during a favorable growing season, the problem is to explain the 1972 curves. One possible explanation is that biomass increment that year was initially very slow due to greater moisture stress, but by mid-August precipitation and saturation deficit were in fact more favorable than in 1973 and more productivity occurred later in the growing season than in 1973.

Both observations, together with the data from Headquarters Park (p. 48), suggest that water stress is an important limiting factor to primary production in alpine and subalpine ecosystems.

In conclusion, my data illustrate the year-to-year variations that may occur in biomass change during the growing season. Unfortunately, two years of data are inadequate for determining either a baseline mean or the range of production variation that is normal.

BIRDS AND MAMMALS

Kenneth L. Diem and Reed W. Fautin

There are many species of birds and mammals in the Medicine Bow Mountains, but little quantitative information has been published. The deer and elk are perhaps best known, probably because they are important game species in the region. Table 13 shows trends in the number of animals harvested since 1950. For reasons not known at this time, the deer harvest has been decreasing while elk harvest has been increasing. The ecology of elk and deer are discussed further beginning on page 105 and 135.

TABLE 13. Deer and elk harvest data[1] on the Medicine Bow National Forest from 1950 to 1970.

Year	Harvest	
	Deer	Elk
1970	4,000	1,350
1965	6,000	950
1960	6,700	150
1955	6,800	50
1950	2,400	70

Tables 14 and 15 are annotated lists of the birds and mammals known to occur in the Medicine Bow Mountains. Estimates of abundance are based on unpublished data and personal observations.

[1] Data collected by the Wyoming Game and Fish Department.

TABLE 14. Species and estimated abundance of birds found in the Medicine Bow Mountains.

Common Name*	Scientific Name*	Estimated Abundance
Mallard	Anas platyrhynchos	Locally common along streams and rivers
American Green-winged Teal	Anas crecca carolinensis	Locally common along streams and rivers
Common Goldeneye	Bucephala clangula	Uncommon on rivers
Common Merganser	Mergus merganser	Fairly common on rivers
Turkey Vulture	Cathartes aura	Locally uncommon
Goshawk	Accipiter gentilis	Uncommon in coniferous forests
Sharp-shinned Hawk	Accipiter striatus	Uncommon
Cooper's Hawk	Accipiter cooperii	Uncommon
Red-tailed Hawk	Buteo jamaicensis	Fairly common
Swainson's Hawk	Buteo swainsoni	Fairly common
Rough-legged Hawk	Buteo lagopus	Fairly common along open foothills
Ferruginous Hawk	Buteo regalis	Uncommon along open foothills
Golden Eagle	Aquila chrysaetos	Uncommon
Bald Eagle	Haliaeetus leucocephalus	Rare along rivers
Marsh Hawk	Circus cyaneus	Fairly common
Prairie Falcon	Falco mexicanus	Uncommon around rocky cliffs
Peregrine Falcon	Falco peregrinus	Very rare
American Kestrel	Falco sparverius	Fairly common
Blue Grouse	Dendragapus obscurus	Common in forested areas
White-tailed Ptarmigan	Lagopus leucurus	Rare on Brooklyn Ridge
Sage Grouse	Centrocercus urophasianus	Uncommon in sagebrush foothills

*Check-List of North American Birds, Committee of the American Ornithologists' Union. Fifth Edition, Baltimore, Maryland. 1957.

Thirty-Second Supplement to the American Ornithologists' Union Check-List of North American Birds. A.O.U. Committee on Classification and Nomenclature, The Auk, Vol. 90, No. 2, pp. 411-419. April 1973.

Corrections and Additions to the Thirty-Second Supplement to the Check-List of North American Birds. A.O.U. Committee on Classification and Nomenclature, The Auk, Vol. 90, No. 4, p. 887. October 1973.

TABLE 14 (continued)

Common Name	Scientific Name	Estimated Abundance
Killdeer	Charadrius vociferus	Uncommon in wet areas of foothills
Common Snipe	Capella gallinago	Uncommon in wet areas
Spotted Sandpiper	Actitis macularia	Fairly common along streams and rivers
Lesser Yellowlegs	Tringa flavipes	Uncommon along streams, rivers and on ponds at lower elevations
California Gull	Larus californicus	Fairly common on lakes and along rivers
Ring-billed Gull	Larus delawarensis	Uncommon on lakes and along rivers
Mourning Dove	Zenaida macroura	Common along foothills
Great Horned Owl	Bubo virginianus	Fairly common
Long-eared Owl	Asio otus	Uncommon along Platte River in willows
Common Nighthawk	Chordeiles minor	Fairly common
White-throated Swift	Aeronautes saxatalis	Uncommon around rocky cliffs
Broad-tailed Hummingbird	Selasphorus platycercus	Common
Rufous Hummingbird	Selasphorus rufus	Uncommon
Belted Kingfisher	Megaceryle alcyon	Fairly common along rivers and streams
Common Flicker	Colaptes auratus	Common
Yellow-bellied Sapsucker	Sphyrapicus varius	Common
Hairy Woodpecker	Dendrocopos villosus	Common
Downy Woodpecker	Dendrocopos pubescens	Common
Northern Three-toed Woodpecker	Picoides tridactylus	Uncommon
Eastern Kingbird	Tyrannus tyrannus	Fairly common at lower elevations
Western Kingbird	Tyrannus verticalis	Uncommon at lower elevations
Say's Phoebe	Sayornis saya	Uncommon at lower elevations
Willow Flycatcher	Empidonax traillii	Common in willows & alders below 9,000 ft.
Gray Flycatcher	Empidonax wrightii	Fairly common
Western Flycatcher	Empidonax difficulis	Fairly common
Western Wood Pewee	Contopus sordidulus	Fairly common
Horned Lark	Eremophila alpestris	Common along foothills and fairly common on Libby Flats

TABLE 14 (continued)

Common Name	Scientific Name	Estimated Abundance
Violet-green Swallow	Tachycineta thalassina	Uncommon around cliffs
Tree Swallow	Iridoprocne bicolor	Fairly common in aspen & cottonwood stands
Bank Swallow	Riparia riparia	Fairly common along rivers
Barn Swallow	Hirundo rustica	Uncommon
Cliff Swallow	Petrochelidon pyrrhonota	Common locally
Gray Jay	Perisoreus canadensis	Common
Steller's Jay	Cyanocitta stelleri	Fairly common
Black-billed Magpie	Pica pica	Common
Common Raven	Corvus corax	Common
Common Crow	Corvus brachyrhynchos	Fairly common at lower elevations
Piñon Jay	Gymnorhinus cyanocephalus	Uncommon at lower elevations
Clark's Nutcracker	Nucifraga columbiana	Common at higher forested elevations
Black-capped Chickadee	Parus atricapillus	Fairly common at lower elevations
Mountain Chickadee	Parus gambeli	Abundant
White-breasted Nuthatch	Sitta carolinensis	Rare
Red-breasted Nuthatch	Sitta canadensis	Fairly common
Pygmy Nuthatch	Sitta pygmaea	Uncommon
Brown Creeper	Certhia familiaris	Fairly common
Dipper	Cinclus mexicanus	Fairly common along streams and rivers
House Wren	Troglodytes aedon	Fairly common
Cañon Wren	Catherpes mexicanus	Rare in river canyons
Rock Wren	Salpinctes obsoletus	Fairly common in rocky areas at lower elevations
Gray Catbird	Dumetella carolinensis	Fairly common in willows and alders
American Robin	Turdus migratorius	Abundant
Hermit Thrush	Catharus guttata	Common locally
Swainson's Thrush	Catharus ustulata	Fairly common
Veery	Catharus fuscescens	Uncommon in willow thickets of lower elevations
Mountain Bluebird	Sialia currucoides	Fairly common
Townsend's Solitaire	Myadestes townsendi	Fairly common locally

TABLE 14 (continued)

Common Name	Scientific Name	Estimated Abundance
Golden-crowned Kinglet	Regulus satrapa	Rare
Ruby-crowned Kinglet	Regulus calendula	Common in coniferous forests
Water Pipit	Anthus spinoletta	Fairly common above timberline
Loggerhead Shrike	Lanius ludovicianus	Fairly common locally
Starling	Sturnus vulgaris	Common locally at lower elevations
Solitary Vireo	Vireo solitarius	Rare
Warbling Vireo	Vireo gilvus	Common in aspens and cottonwoods at lower elevations
Yellow Warbler	Dendroica petechia	Abundant in willow-alder habitat
Yellow-rumped Warbler	Dendroica coronata	Common locally in coniferous forests
MacGillivray's Warbler	Oporornis tolmiei	Fairly common in riparian thickets
Common Yellowthroat	Geothlypis trichas	Fairly common in riparian thickets
Wilson's Warbler	Wilsonia pusilla	Fairly common in riparian thickets at higher elevations
Western Meadowlark	Sturnella neglecta	Common along open foothills
Northern Oriole	Icterus galbula	Fairly common along rivers at lower elevations
Brewer's Blackbird	Euphagus cyanocephalus	Common in wet areas of lower elevations
Brown-headed Cowbird	Molothrus ater	Fairly common at lower elevations
Western Tanager	Piranga ludoviciana	Fairly common in coniferous areas
Black-headed Grosbeak	Pheucticus melanocephalus	Uncommon along Platte River
Lazuli Bunting	Passerina amoena	Uncommon along streams & rivers at lower elevations
Evening Grosbeak	Hesperiphona vespertina	Uncommon
Cassin's Finch	Carpodacus cassinii	Fairly common in conifers
Pine Grosbeak	Pinicola enucleator	Fairly common in conifers
Brown-capped Rosy Finch	Leucosticte australis	Uncommon in alpine or artic zones
Pine Siskin	Spinus pinus	Abundant in coniferous forest
American Goldfinch	Spinus tristis	Common in weedy and forested foothills

TABLE 14 (continued)

Common Name	Scientific Name	Estimated Abundance
Red Crossbill	Loxia curvirostra	Fairly common locally
Green-tailed Towhee	Chlorura chlorura	Fairly common in foothill shrub habitat
Lark Bunting	Calamospiza melanocorys	Uncommon along open foothills
Vesper Sparrow	Pooecetes gramineus	Common in shrub-steppe
Gray-headed Junco	Junco caniceps	Common
Chipping Sparrow	Spizella passerina	Common
Brewer's Sparrow	Spizella breweri	Abundant in shrub zone of foothills
White-crowned Sparrow	Zonotrichia leucophrys	Common at higher elevations
Lincoln's Sparrow	Melospiza lincolnii	Common in shrubs at higher elevations
Song Sparrow	Melospiza melodia	Common in willow & alder habitat

TABLE 15. Species and estimated abundance of mammals found in the Medicine Bow Mountains.*

Common Name*	Scientific Name*	Estimated Abundance
Masked Shrew	Sorex cinereus cinereus	Most common in coniferous forests
Vagrant Shrew	Sorex vagrans obscurus	Most widely distributed shrew in Wyoming
Dwarf Shrew	Sorex nanus	Rare
Water Shrew	Sorex palustris navigator	Common along streams in dense herbaceous vegetation
Little Brown Myotis	Myotis lucifugus carissima	Rare even at lower elevations
Long-legged Myotis	Myotis volans interior	Fairly common at lower elevations
Big Brown Bat	Eptesicus fuscus pallidus	Uncommon
Pika	Ochotona princeps saxatilis	Fairly common talus slopes and rock piles
Nuttall's Cottontail	Sylvilagus nuttallii grangeri	Rare in forested area
Snowshoe Rabbit	Lepus americanus bairdii	Fairly common in forested area
White-tailed Jack-rabbit	Lepus townsendii campanius	Uncommon on Libby Flats, but common on plains
Black-tailed Jack-rabbit	Lepus californicus melanotis	Rare even on plains
Least Chipmunk	Eutamias minimus operarius	Common at all elevations
Uinta Chipmunk	Eutamias umbrinus montanus	Rare in Albany County
Yellow-bellied Marmot	Marmota flaviventris luteola	Common
Richardson's Ground Squirrel	Spermophilus richardsonii elegans	Common in brush of foothills; present on Libby Flats
Thirteen-lined Ground Squirrel	Spermophilus tridecemlineatus pallidus	Common on Laramie plains
Golden-mantled Ground Squirrel	Spermophilus lateralis lateralis	Common
White-tailed Prairie Dog	Cynomys leucurus	Locally uncommon on Laramie plains area
Red Squirrel	Tamiasciurus hudsonicus fremonti	Common
Northern Pocket Gopher	Thomomys talpoides rostralis	Common in non-forested area at all elevations
Beaver	Castor canadensis missouriensis	Fairly common along rivers and streams
Western Harvest Mouse	Reithrodontomys megalotis dychei	Fairly common in non-forested area at lower elevations

*Nomenclature follows that of Long (1965).

Long, Charles A. 1965. The Mammals of Wyoming, Univ. of Kan. Pub. 14(18):493-758.

TABLE 15 (continued)

Common Name	Scientific Name	Estimated Abundance
Deer Mouse	Peromyscus maniculatus nebrascensis	Very abundance
Northern Grasshopper Mouse	Onychomys leucogaster arcticeps	Fairly common in grassland
Bushy-tailed Wood Rat	Neotoma cinerea orolestes	Uncommon
Red-backed Vole	Clethrionomys gapperi galei	Common in lodgepole pine and spruce-fir forests
Heather Vole	Phenacomys intermedius intermedius	Uncommon
Montane Vole	Microtus montanus nanus	Abundant
Long-tailed Vole	Microtus longicaudus longicaudus	Rare
Sagebrush Vole	Lagurus curtatus levidensis	Rare
Muskrat	Undatra zibethicus cinnamominus	Common along streams
Western Jumping Mouse	Zapus princeps princeps	Common along streams with dense herbaceous vegetation
Porcupine	Erethizon dorsatum bruneri	Common in coniferous forests
Coyote	Canis latrans latrans	Common
Red Fox	Vulpes vulpes regalis	Common
Swift Fox	Vulpes velox velox	Very rare
Black Bear	Ursus americanus cinnamomum	Locally fairly common
Raccoon	Procyon lotor hirtus	Common along North Platte with ranges extending to about 8,300 along Big and Little Laramie Rivers
Marten	Martes americana origenes	Common in coniferous forests but not readily seen
Ermine	Mustela erminea muricus	Rare -- above 10,000 feet
Long-tailed Weasel	Mustela frenata nevadensis	Common
Mink	Mustela vison letifera	Fairly common along rivers and streams of lower elevations
Badger	Taxidea taxus taxus	Common
Striped Skunk	Mephitis mephitis hudsonica	Common

TABLE 15 (continued)

Common Name	Scientific Name	Estimated Abundance
Mountain Lion	Felis concolor hippolestes	Rare
Lynx	Lynx canadensis canadensis	Rare
Bobcat	Lynx rufus pallescens	Locally common
Wapiti	Cervus canadensis nelsoni	Common
Mule Deer	Odocoileus hemionus hemionus	Common
White-tailed Deer	Odocoileus virginianus dacotensis	Uncommon, along flood plains at lower elevations
Pronghorn	Antilocapra americana americana	Locally common along foothill region
Mountain Sheep	Ovis canadensis canadensis	Fairly common along Platte River Canyon around Douglas Creek

LAKE FISHERIES

George Baxter

There are over 80 lakes in the Medicine Bow Mountains, and hundreds of small ponds on the glacial moraines and outwash aprons. About half are alpine or subalpine lakes which are relatively deep (over 15 m maximum depth) with a surface area of from 10 to 50 hectares. These lakes are drainage lakes whose basins were formed by glacial digging. The bottom type in general is partly boulders with silt in the deeper areas; vascular aquatic vegetation is generally sparse and very little is known about it. When either the inlet or outlet stream is accessible to trout and has some gravels, reproduction by brook trout migrating from the lake is adequate to maintain the brook trout fisheries without supplemental stocking. Examples are Libby Lake, Lake Marie, Big Brooklyn Lake, and Big and Little Telephone Lakes.

Another category of lakes includes the smaller (<10 ha), shallow, mud-bottomed lakes with somewhat warmer temperatures, more aquatic vegetation and often quite dense fish populations, again depending upon adequate spawning habitat. Examples are Towner Lake, Little Brooklyn Lake and Mill Pond, all of which have man-made dams and are situated at about 3100 to 3200 m. Some of the smaller lakes have an inadequate volume of flowing water and are marginal for trout fisheries; others do not support any fish.

Some lakes have a very rapid flushing rate (see p. 259). For example, Little Brooklyn Lake loses as much water in 10 to 72 hours as the lake can hold. This same lake has a very low phytoplankton biomass (ca 220,000 u^3 ml^{-1}) and a low productivity of about 100 mg carbon per m^3 per day. Some of the lakes may stratify thermally, but such stratification is usually unstable and short-term. Anoxic conditions

may develop and some lakes freeze solid.

The Medicine Bow Mountains have no native trout. The brook trout was introduced into the Mountains in about 1885 and the rainbow, brown, and cutthroat trouts were introduced shortly thereafter. In more recent years the golden trout and the Arctic grayling have been planted in a few habitats. The longnose sucker and the white sucker are native, are common in all the lakes, and are present in varying abundance in the streams. Three native minnows -- the creek chub, the fathead minnow, and the longnose dace -- are present but are only rarely found above 2700 m.

At present the brook trout predominates in waters above 2700 m where it is the only trout with good reproductive success. The cutthroat and rainbow trouts have been maintained by stocking in selected lakes; the survivors from these stocked fish experience limited reproduction in some habitats. In the larger streams in the lower montane and foothills zones, the brown trout and rainbow trout have established self-maintaining populations, and mixed fisheries of brook, brown and rainbow trout with an occasional cutthroat or rainbow-cutthroat hybrid occur. The relative abundance of the three species in a particular habitat is probably determined by the combination of water temperature, low temperatures favoring the brook trout; cover, which is required by the brown trout; and stream velocity, torrential waters being preferred by the rainbow.

Fishing pressures are light to moderate depending upon accessibility, but have increased steadily in the last several decades. Fishing and natural mortalities coupled with slow growth at prevailing water temperatures limit the age and growth of trout. Fish over five years of age are rare and the fisheries are characterized by generally small fish. Nonetheless, the populations are relatively dense and recreational fishing is popular in the area. A few experiments on lake fertilization have not resulted in increased fish growth (Baxter 1955), but the fish do grow larger when competition is reduced. Fish drift and invertebrate drift are both very important in the streams and could be affected by a winter precipitation management program (see p. 255).

Early studies of the biology of brook trout in the Snowy Range were made by Holland (1927), Glass (1934), Fleming (1939), and Fautin (1951). Felix Simon (1938) published the results of a lake and stream survey of the Snowy Range, including an account of the fisheries of all the major lakes and streams and some management recommendations. Wyoming Game and Fish Department personnel surveyed the fisheries of the area again in the period 1956-1962 and again in 1974, reporting on 80 lakes and all major streams, and including information on fish populations, food, and water chemistry.

Growth. The lakes and streams of the Snowy Range have generally cold water, short growing seasons, low nutrient content, and relatively dense fish populations, all of which are conducive to relatively slow growth of trout. The growth rates of brook trout from three lakes are given in Table 16 and growth curves of these populations and from three stream populations are plotted in Fig. 19. Although some differences are seen between lake and stream habitats, the general trends are quite consistent.

Fish in the creel from the lake fisheries are mostly Age II and Age III brook trout ranging in size from 175 mm to 260 mm. In the accessible and moderately heavily-fished lakes, brook trout over Age V which reach a size of some 300 mm usually make up less than 5% of the populations. Growth rates in the Snowy Range are essentially similar to those of other brook trout populations in the Rocky Mountains (Carlander 1969, pp. 244-267).

Stock Densities and Production. Fish biomass and population structure for several lakes are presented in Table 17. Stock densities in kg/hectare for Libby Lake, Towner Lake, and Little Brooklyn Lake were, respectively, 29.2, 34.6, and 14.4.

Among the calculations of net production, those for Towner Lake are based upon the most accurate and complete data. In that lake the population estimates were repeated for several years as were age-growth determinations. The major weaknesses of the Libby Lake data for production calculations are in the estimates of numbers of the Age 0 and the Age IV and older fish. Because the total production of these

ages is relatively small, due to the small size of the young-of-the-year fish and the small numbers of the older fish, the errors in the estimates of total production are not large. The estimates of production are 17.7 kg/ha/yr in Libby Lake and 40.6 kg/ha/yr in Towner Lake.

Food and Feeding. Food studies were done by Hepworth (1958), Royer (1960), Sinn (1960), and Garofalo (1964). During the period of study (1957-1964), the most important food organisms in the lakes were from the benthos (Table 18): midge larvae and pupae, leeches and snails; from the open water: zooplankton, cladocera and some copepoda; and from the surface: adult terrestrial and aquatic insects. Fish and bristleworms (Oligochaeta) were almost never encountered in the stomachs of lake brook trout. Food varied with season; in June and July midges predominated in the diet, but later zooplankton and terrestrial insects were more important. Mollusca, primarily snails of the genera Physa and Planorbis were much more important in Little Telephone than in Towner Lake. Interestingly, Garofalo (1964) found more mollusca (Genus Physa) in the stomachs of female trout than in the stomachs of male trout, a finding which has not been carefully checked in subsequent studies.

Stomach contents relative to availability are more difficult to assess in lakes than in streams. Garofalo (1964) measured emergence of midges with emergence traps, but the relative availability of leeches, molluscs and terrestrial insects has not been evaluated.

Reproduction. Near the Snowy Range male brook trout may become sexually mature at Age I+, approximately 17 months after hatching. The smallest sexually mature male observed by Christensen (1965) was 99 mm in length. In 1963, using an upstream migration trap in the stream above Towner Lake, he collected 63 ripe males of Age I+, ranging in length between 99 mm and 137 mm (3.9"-5.4") among a total of 444 sexually mature males captured. Most males do not reach sexual maturity until Age II+. The youngest sexually mature females encountered by Christensen (1965) or Hepworth (1959) were Age II+; the smallest sexually mature female collected by Christensen was 142 mm (5.6") in length.

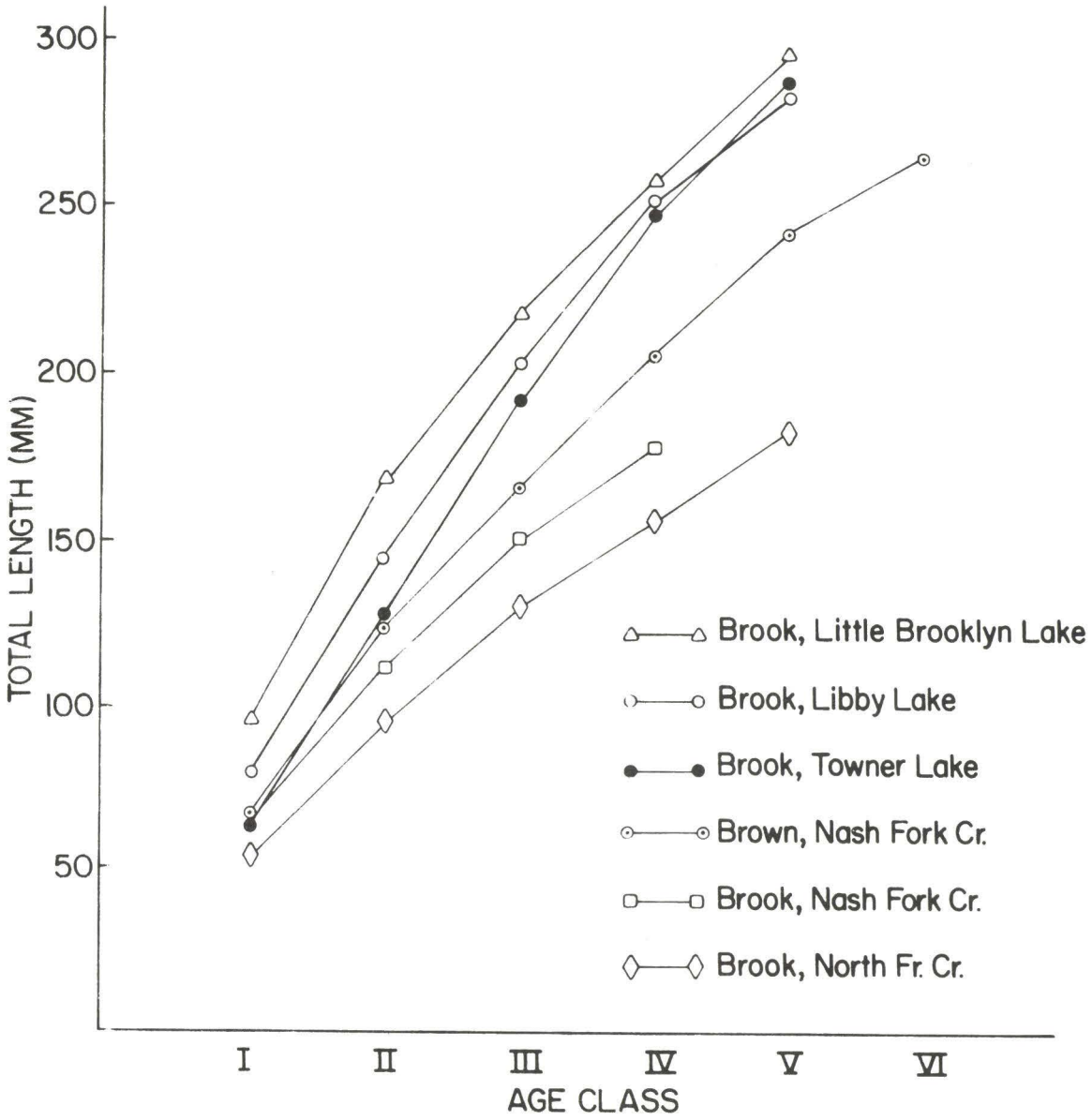

Fig. 19. Growth of trout in several different habitats in the Medicine Bow Mountains.

The spawning migration upstream from Towner Lake continues from early September into October, when heavy snows make further study impossible (Christensen 1963). Water temperatures ranged from 10°C to 14°C. Males migrated earlier than females and moved further upstream. The number of eggs produced varied from about 210 for 152 mm females to 1200 for females 304 mm and longer in total length.

Christensen (1965) studied the growth of fry in Towner Lake and in a beaver pond upstream from the lake through which the spawning migration passes and which acts as a catch-basin for downstream drifting fry. Slower growth of fry in the beaver pond as compared with fry in Towner Lake was thought by Christensen to be due to crowding. White (1965) continued observations on fry drift in 1964. It is evident from these studies that beaver ponds and the variety of man-made and natural (moraine) lakes in the stream drainages act as catch basins for the downstream drift of brook trout fry and fingerlings. Winter cloud seeding could increase the mean yearly amount of downstream drift which could be significant to the fishery.

TABLE 16. Total length (mm) and weight (g) at successive ages of brook trout from four lakes.

	Libby Lake (Sinn, 1961)		Towner Lake*		Little Brooklyn Lake (Royer, 1959)		Little Telephone Lake (Hepworth, 1959)	
Age	L	W	L	W	L	W	L	W
0+	71	3.6	65	1.2	97	-	58	-
1+	145	31.3	128	19.9	170	-	140	-
II+	203	86.6	192	69.8	218	-	203	-
III+	251	163.7	248	146.5	258	-	260	-
IV+	282	230.4	287	209.1	296	-	300	-

* Mean of several studies.

TABLE 17. Estimated numbers by age group of brook trout in 3 lakes, and biomass in kg/ha.

Age	Towner Lake[1] (3.56ha)	Little Brooklyn[2] (3.2ha)	Libby Lake[3] (10.32ha)
0+	2006	870	-
1+	1873	1051	542
II+	712	680	1673
III+	197	107	935
IV+	27	22	277
V+			65
biomass, kg/ha	34.6	14.4	29.2

1 Mean of estimates made in 1958 (Hepworth 1959), 1959 (Royer 1960), 1962 (Garofalo 1964), 1965 (Christensen 1965), and 1964 (White 1965).

2 Mean of estimates made in 1959 (Royer 1960) and 1962 (Garofalo 1964).

3 Mean of estimates from Sinn (1961).

TABLE 18. Food of brook trout in lake habitats near the Snowy Range axis in the Medicine Bow Mountains, expressed as estimated percentage of total volume of major food components.

	LL[1]	LTL[2]	TL[3]	T2[4]	T3[5]	LB1[6]	LB2[7]
Midge	15.0	19.2	59.8	48.4	59.5	44.3	42.7
Mixed Aquatic[8]	1.8	25.9	13.9	7.6	13.0	10.6	16.3
	12.0	25.6	10.7	7.4	26.5	29.8	19.7
Terrestrial Insects	10.6	23.5	17.0	19.7	5.0	5.7	1.7

1 Libby Lake (Sinn 1961)
2 Little Telephone Lake (Hepworth 1958)
3 Towner (Hepworth 1958)
4 Towner (Royer 1959)
5 Towner (Garofalo 1962)
6 Little Brooklyn (Royer 1959)
7 Little Brooklyn (Garofalo 1962)
8 Snails, leeches, water mites, amphipods, caddis flies

HUMAN UTILIZATION

Dennis H. Knight

Human utilization of the mountains is extensive. Being almost entirely in the Medicine Bow National Forest, the land is subject to multiple use which includes recreation, grazing of sheep and cattle, lumbering, wildlife, and water. Roads penetrate most of the area, permitting easy access for most uses. Skiing and snowmobiling are very popular during the winter; and Douglas Creek, French Creek, and the North Platte River are considered to be among the best trout streams in the state, if not the nation. At the present time there is considerable debate over how the Medicine Bow National Forests should be used, whether to emphasize lumber, recreation, or water. Any cloud-seeding program is likely to meet with considerable discussion by many people with special interests in the area. Multiple use requires compromises that are becoming more and more difficult with greater resource demands from more and more people. Although the population density in the immediate area is low, the Medicine Bow Mountains are a major recreation area for the developing megalopolis along the foothills of the Colorado front range.

Table 19 summarizes some data on human utilization in the Medicine Bow Mountains of Wyoming. Data such as in Table 19 are available also for specific areas within the Mountains, and for specific activities. An increase of recreational use is apparent from the data. Winter visitor days accounted for about 8 percent of the total in 1970.

The following data illustrate timber harvest trends in the entire Medicine Bow National Forest, which includes the Laramie Peak Division, Pole Mountain Division, and the Hayden Division, but it is thought that the same trends apply to the Medicine Bow Mountain Division.

	1969	1970	1971	1972	1973	1974
CLEAR-CUT ACRES FOR LUMBER	2,584	1,778	2,318	2,980	3,021	1,370
PARTIAL-CUT ACRES FOR LUMBER	699	608	381	1,850	3,013	2,979

Figs. 20 and 21 show trends for actual cut of timber (board feet) and actual use by sheep and cattle (animal months). Timber harvest is now higher than in the late 1960's, but not as high as during 1956, 1957, and 1960. Grazing pressure by cattle has remained quite constant since the early 1960's, but the number of sheep has dropped dramatically, apparently due to poor market conditions.

With regard to the effect of increased snowfall on human utilization, the major expressed concern would probably center on how long spring access would be delayed. Cattlemen would probably not object, assuming they are convinced that cloud seeding will not cause flooding or snow accumulation below 2700 m, since their animals graze and calve at lower elevations. Sheep, however, use the high elevation meadows and already are restricted to a period of less than 2 months (mid-July to early September) due to weather and range conditions. Some lumbermen will be concerned about possible delayed access to logging roads.

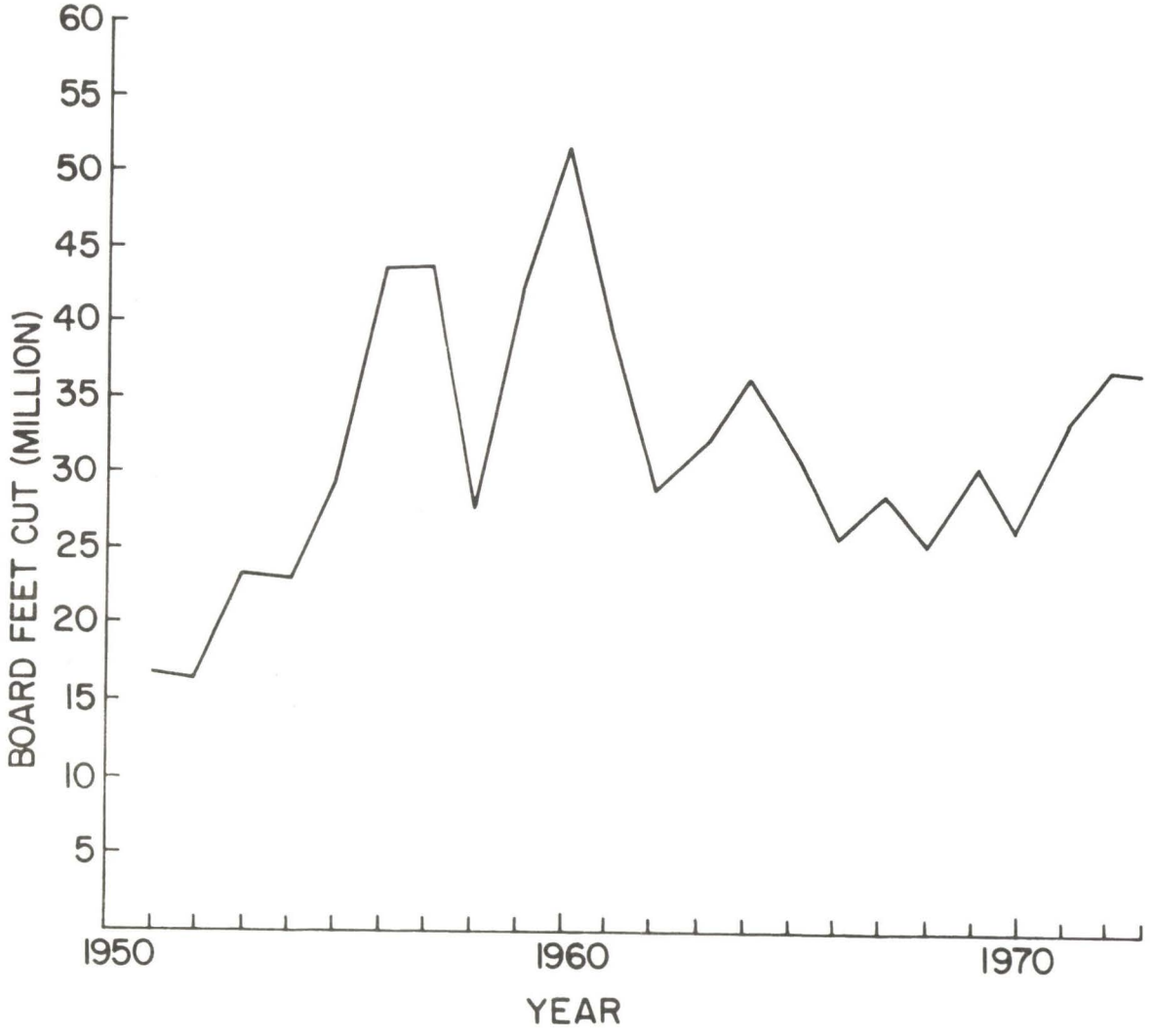

Fig. 20. Annual timber harvest in the Medicine Bow National Forest since 1951. Data from Supervisor's Office, Medicine Bow National Forest, Laramie, Wyoming.

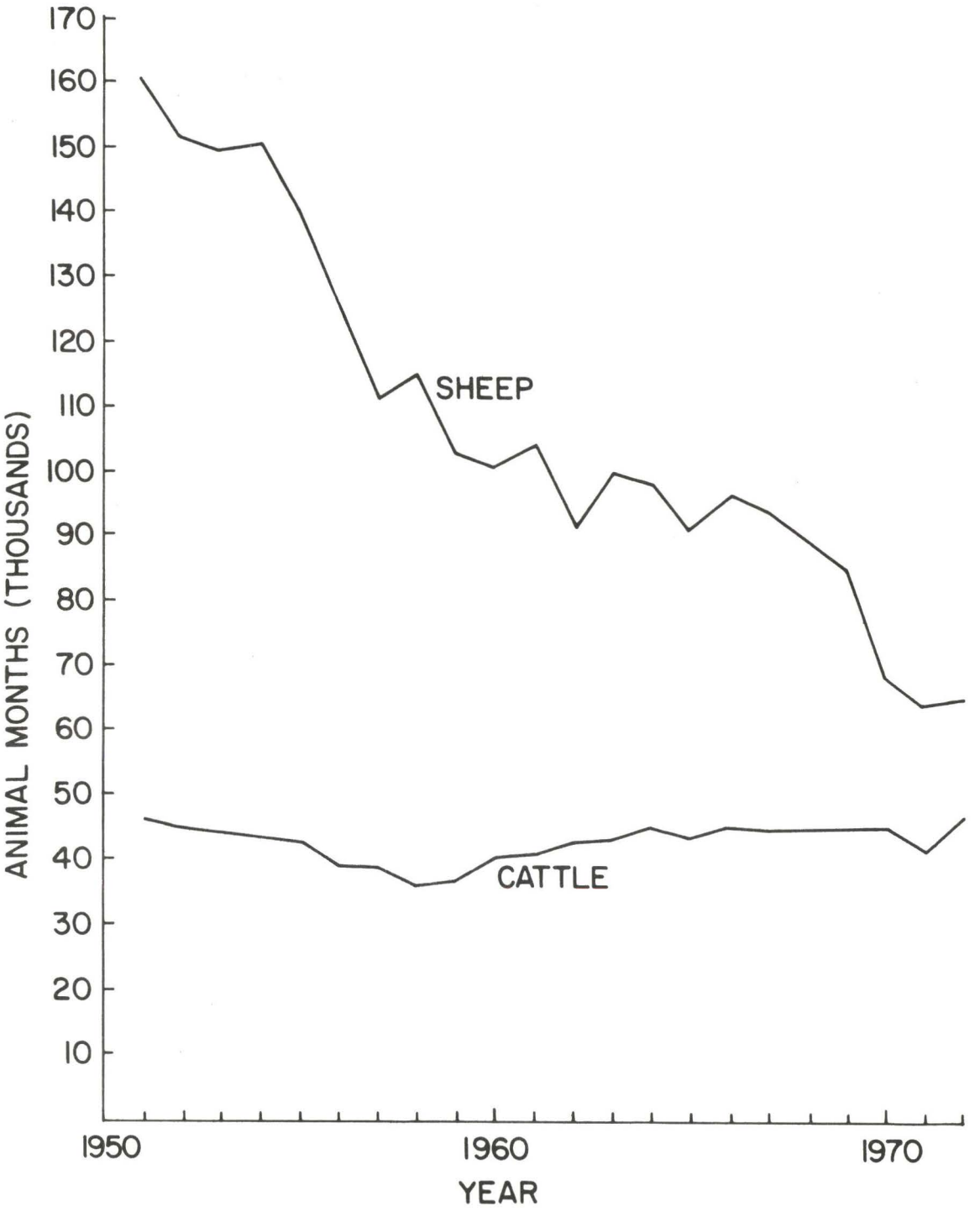

Fig. 21. Range use by sheep and cattle since 1951 in the Medicine Bow National Forest. Data from the Supervisor's Office, Medicine Bow National Forest, Laramie, Wyoming.

TABLE 19. Some data on human utilization of the Medicine Bow Mountains in Wyoming. Source: Supervisor's Office, Medicine Bow National Forest, Laramie 82070.

USE	YEAR			
GRAZING PERMITS	1971	1972	1973	1974
Number of cattle and horse grazing allotments	17	18	18	18
Number of sheep and goat allotments	15	15	15	15
Number of cattle and horse animal unit-months	11,308	11,185	12,542	11,750
Number of sheep and goat animal unit-months	23,276	17,277	16,358	16,358
Number of cattle permitted	3,439	3,399	3,886	3,620
Number of sheep permitted	14,057	10,133	9,233	9,233
TOTAL VISITOR DAY USE	324,000	384,700	416,600	386,000
VISITOR DAY USE BY HUNTERS AND FISHERMAN	50,100	54,000	58,800	--

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THE IMPACT OF SNOW ON ELK

A. L. Ward, K. Diem, and R. Weeks

Late fall, winter, and early spring seasons represent stressful times for elk in the Central and Northern Rocky Mountains. A variety of natural and man-induced factors affect the animals, and snow accumulation is known to be an important cause of stress. If elk populations are affected by additional snowfall from cloud seeding, the type and degree of that change can be determined only through comparison to some established frame of reference. Therefore, this study had the following objectives:

1. Development of pre-cloud seeding baseline inventory data, i.e. population numbers, composition, movement, and distribution on their seasonal ranges.
2. Identification, description and, where possible, measurement of the various factors (with special emphasis on snow) which influence the movement, distribution, and general welfare of elk.

Review of Other Relevant Research

Only limited information is available on the response of elk to snow accumulation. Gaffney (1941) stated that the amount of snow in which elk can winter successfully depends on several factors: 1) the composition, height, and volume of the palatable vegetation; 2) condition of snow--packed, crusted, or loose; 3) age and condition of the animals; and 4) topography and weather conditions. He found on

the south fork of the Flat-head River, Montana, that elk often nosed through 30 to 46 cm of loose snow while feeding on bunchgrass and frequently pawed to obtain food in 91 cm of moderately loose snow. He concluded that generally 122 cm of snow represents the maximum in which the elk can range efficiently and that they will buck 30 to 46 cm more snow on the flats than on a hillside. Anderson (1954) found that snow depths of 15 to 25 cm started mass migration of elk out of Yellowstone Park toward the lower elevations of Jackson Hole, and Murie (1951) stated that "all the evidence obtainable, including all field observations, indicates that in the fall snow is the chief causative factor of elk migrations."

Kelsall and Telfer (1971) point out that Russian studies suggest the importance of chest heights and weight loads on tracks when assessing mammal tolerance to varied snow conditions. Their preliminary results suggest that in deep, soft snow the older animals, particularly males, have an advantage, and that moose and elk have a locomotive advantage over white-tailed deer and bison. They also recognized that animal behavior, in the form of habitat selection and methods of feeding, also helps to determine interrelationships between animals and snow cover.

Study Area

A study area with about 700 elk was located on the west side of the Medicine Bow Mountains, from French Creek south to the Colorado-Wyoming state line. Though these elk are in this area in late fall, winter, and spring, they disperse over a much larger area during the summer. Elevation ranges from 2248 m where French Creek meets the North Platte River to 3660 m at the top of Medicine Bow Peak. Elk winter range for the past eight years has been below 2743 m on both the east and west side of the Range.

Methods

A telemetry system (Weeks et al. 1972a, 1972b) and visual observation were used to gather information on elk distribution and

activity. The use of telemetry is valuable, not only in helping to locate instrumented elk but also, since elk are gregarious, the groups with which the individuals associate.

Thirty elk were live-trapped in a corral trap on the west side of the North Platte River during the two winters of 1971-72 and 1972-73. Seven cows were fitted with telemetry collars and 13 (10 cows and 3 female calves) were fitted with individually-numbered neck collars during March and April, 1972. One cow was fitted with a transmitter collar and 4 cows and 3 female calves fitted with numbered collars on December 6, 1972. Two adult cows were fitted with telemetry collars on May 16, 1973. The transmitter collars weighed about 1020 grams each and were set to six different frequencies. Transmitter life ranged from 2.5 to 21 months. Because of the difficulty of finding the high frequency radio signals on the ground during summer and fall, telemetered elk were located from the air at weekly intervals using methods described by Craighead et al. (1971). From June to October we made 22 flights in 1972 and 21 in 1973. Most of the data were obtained in the early morning or late evening when the elk were feeding.

Vegetation on elk feeding sites was measured using the canopy-coverage method described by Daubenmire (1959). Food eaten by elk on the winter range was determined by collecting fresh fecal droppings and using microtechniques described by Ward (1970) to identify graminoids, forbs, sagebrush, and other browse. Time-lapse photography systems utilizing super-8 mm movie cameras and 35 mm time-lapse cameras (Diem et al. 1973) were used to monitor elk use and snow depths on specific elk feeding sites on both winter and summer ranges.

Snow depths and densities were measured at selected elk feeding sites (Table 20) using a metal probe and a standard Mount Rose (Federal) sampler. At each feeding site ten stations were sampled for density spaced 10 paces apart along a transect running perpendicular to the slope, and five snow depth measurements were made at each station. Analysis of variance and Duncan's multiple range tests were used to determine significant differences in snow depths and

Table 20. Snow course and elk winter feeding areas. See also the aerial photo in Fig. 22.

Number on aerial photo	General Description	Aspect	Percent slope	Degrees	Cover vegetation
1	Trap site	235° (WSW)	12	10.8	Sage-grass
2	Aspen grove near trap	243° (WSW)	3	2.7	Aspen-sedge
3	Lodgepole pine near trap	356° (N)	12	10.8	Lodgepole
4	Upper 35 mm camera site	223° (SW)	6	5.4	Sage-grass
5	Lower 35 mm camera site	221° (SW)	46	41.4	Sage-grass
6	Feeding site near beaver dam	138° (SE)	42	37.8	Sage-grass
7	West facing near North Platte	270° (W)	39	35.1	Sage-grass
8	Road near North Platte River	335° (NNW)	6	5.4	Grass
9	East facing near North Platte	85° (E)	45	40.5	Sage-grass
10	Mouth of Douglas Creek	190° (S)	55	49.5	Sage-grass
11	Steep slope east side river	180° (S)	60	54.0	Sage-grass
12	Boat Creek access road	190° (S)	34	30.6	Sage-grass
13	Cottonwood Creek	172° (SSE)	34	30.6	Sage-grass
14	Savage Run	172° (SSE)	40	36.0	Sage-grass
15*	Ridge top west of trap	325° (NW)	6	5.4	Sage-grass
16*	Deerhorn Point	190° (S)	2	1.8	Sage-grass
17*	Near Highway 230	270° (W)	5	4.5	Sage-grass

*Locations not shown in aerial photo.

water between areas and time of sampling. Transects in the same area but off-set to keep from hitting the same holes were made at various times during the winter of 1972-73.

Aerial photographs (Fig. 22) of the elk winter range within 1.6 km of the elk trap along the North Platte River were taken on April 5, 1973 by the Wyoming Highway Department photo crew. These photos show snow-accumulation areas and snow-free areas. A helicopter flight was made on April 13, 1973 to count elk distribution in relation to snow distribution.

Three weather stations were maintained during the winter of 1972-73 to record temperature, relative humidity, wind, and solar radiation. The stations were located in 1) heavy lodgepole pine timber on a north-facing slope, 2) an aspen stand on a gentle west-facing slope, and 3) an exposed ridge top. All measurements were continuously recorded on graphs except wind which was registered on a dial and read at regular intervals or when personnel were in the area.

Percent of total radiation received, as influenced by cloud cover, was calculated by averaging recorded radiation for seven-day periods, including the eight dates used by Buffo et al. (1972), and dividing by the maximum radiation recorded for a clear day during the period. The value of direct solar radiation for corresponding slope, aspect, and dates at latitude 40 degrees north as given by Buffo et al. (1972) were then calculated for each of the sites where some snow depth data were taken. Solar radiation at 40° latitude reaches its highest values (584 to 724 cal/cm^2/day) on 60-degree south-facing slopes during December, January, and February, while at the same time 45-degree north-facing slopes are receiving no direct solar radiation.

Results

Elk Census Data

Aerial flights have been made every winter since 1968 to observe elk distribution and numbers on the winter range between Camp Creek in Colorado and French Creek in Wyoming along both sides of the North

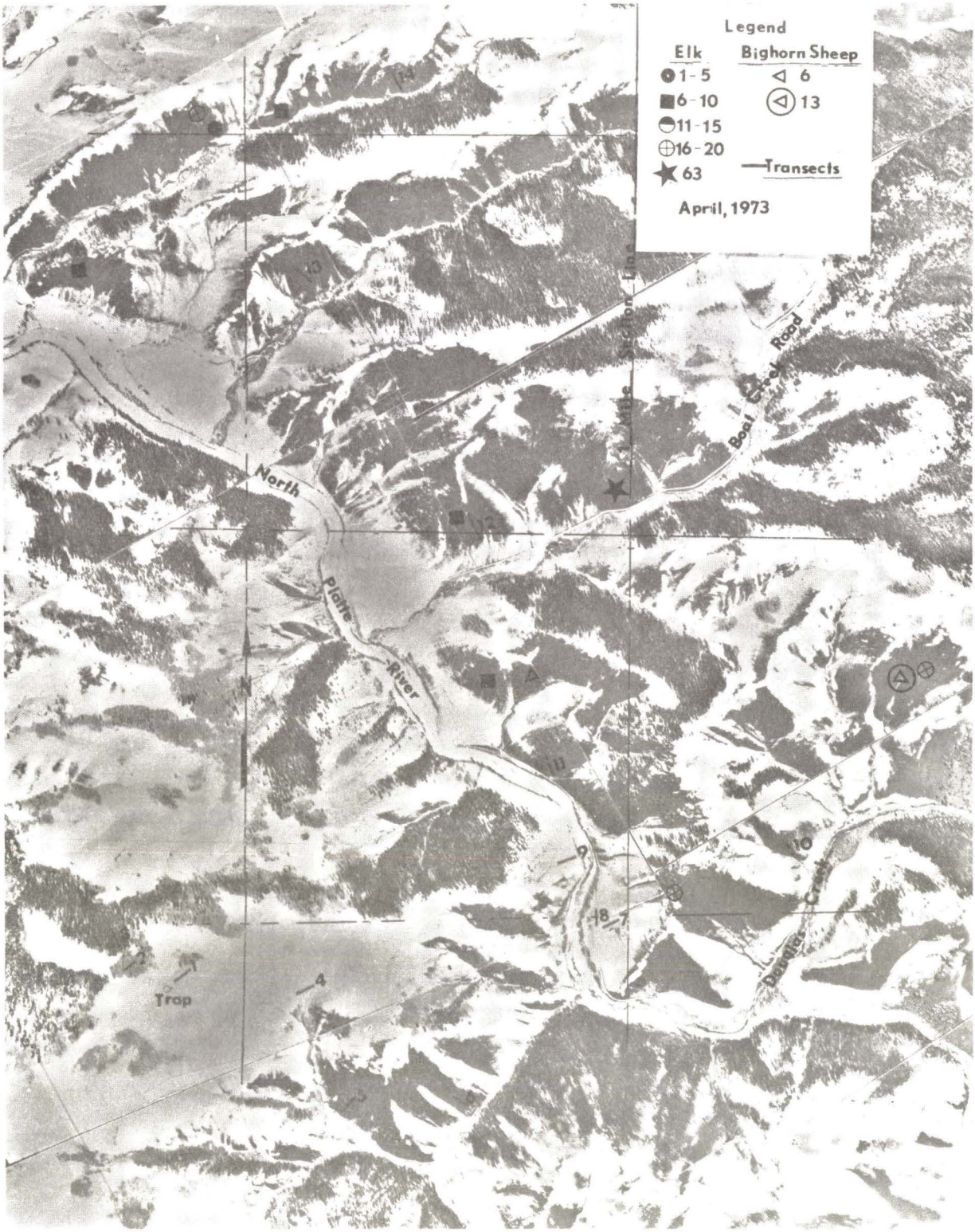

Fig. 22. Aerial photograph of winter elk range, taken April 5, 1973

Platte River. This area covers a distance of about 32 airline km over approximately 104 km^2 of rather steep, rough topography. Maximum elk counted each year were as follows:

Date	Total elk	East of river	West of river
Feb. 1968	296	261	35
Jan. 1969	412	412	0
Mar. 1970[1]	455	357	98
Feb. 1971[2]	457	--------No record---------	
Feb. 1972	701	497	204
Apr. 1973[1]	514	437	77
Apr. 1974[1]	551	537	14

There is a definite trend of increasing elk numbers on this range. Harvest figures published by the Wyoming Game and Fish Commission show this same trend with the exception that harvest declined from 462 in 1972 to 390 in 1973.

The number of elk seen on the west side of the North Platte River is greater in years when the snow depths along the North Platte River at the mouth of Douglas Creek are lowest. The elk are able to utilize forage on the more level, gentle habitat on the west side of the river when the snow is shallow and more feed is available.

Summer Elk Distribution

Elk distribution over the major portion of the summer range in 1972 is shown in Fig. 23. Two elk collared with telemetry transmitters the same day spent the summer at the two opposite extremes of the summer range, about 19 to 22 km apart. Elk from one trap site on

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[1]Helicopter (all other counts made in Wyoming Game and Fish L-19 airplane); due to fuel supply the trip length was somewhat less.

[2]Wyoming Game and Fish Commission data.

Fig. 23. Elk distribution during the summer of 1972.

the winter range distributed themselves over the south end of the Medicine Bow Range in summer. The largest group (52 cows, 29 calves and 3 small bulls) was observed with telemetered Cow 1 in Nelson Park, a large subalpine park at 3140 m on July 12. The average number of elk seen with a telemetered cow was 17 (range 1 to 84).

Cow 3 was monitored for two summer seasons. Her range for the 21-month period of transmitter life is shown in Fig. 24. She used about the same range both summers which covered approximately 52 km^2. The average number of elk seen with Cow 3 over the 21-month period was 11.2 (range 2 to 50).

During the summers of 1972 and 1973 there were 1,754 and 676 elk seen, respectively (many were seen several times). The three new telemetered cows, one trapped in December 1972 and two in May 1973, spent the summer of 1973 in the Devil Gate-Hans Creek area where they were very difficult to observe.

Elk prefer to keep about 0.8 km distant from people who are engaged in out-of-vehicle activity such as harvesting timber, clean-up operations, or various types of recreation. Elk can be expected to move back into the area after the timber harvest and clean-up. Traffic on Forest Service roads has little effect on elk activity, especially beyond 275 m. The major concern is to keep roads away from elk feeding sites on open meadows and slopes, along stream courses, and adjacent to clearcut timber harvest sites that have palatable elk forage growing in them (Ward 1973, 1974).

The fall snow storms had a definite effect on moving elk to the lower country, an observation made by others also. Even a 10 to 15 cm snow cover moved animals from the higher parks. During the hunting season there were some movements back into the deeper snow, which is probably a direct result of the presence of hunters. Elk were rarely seen feeding on open slopes after the opening of deer and elk hunting seasons in October. Elk were seen only in the more remote areas, and they seemed reluctant to leave the dense lodgepole pine where they retreat when being hunted.

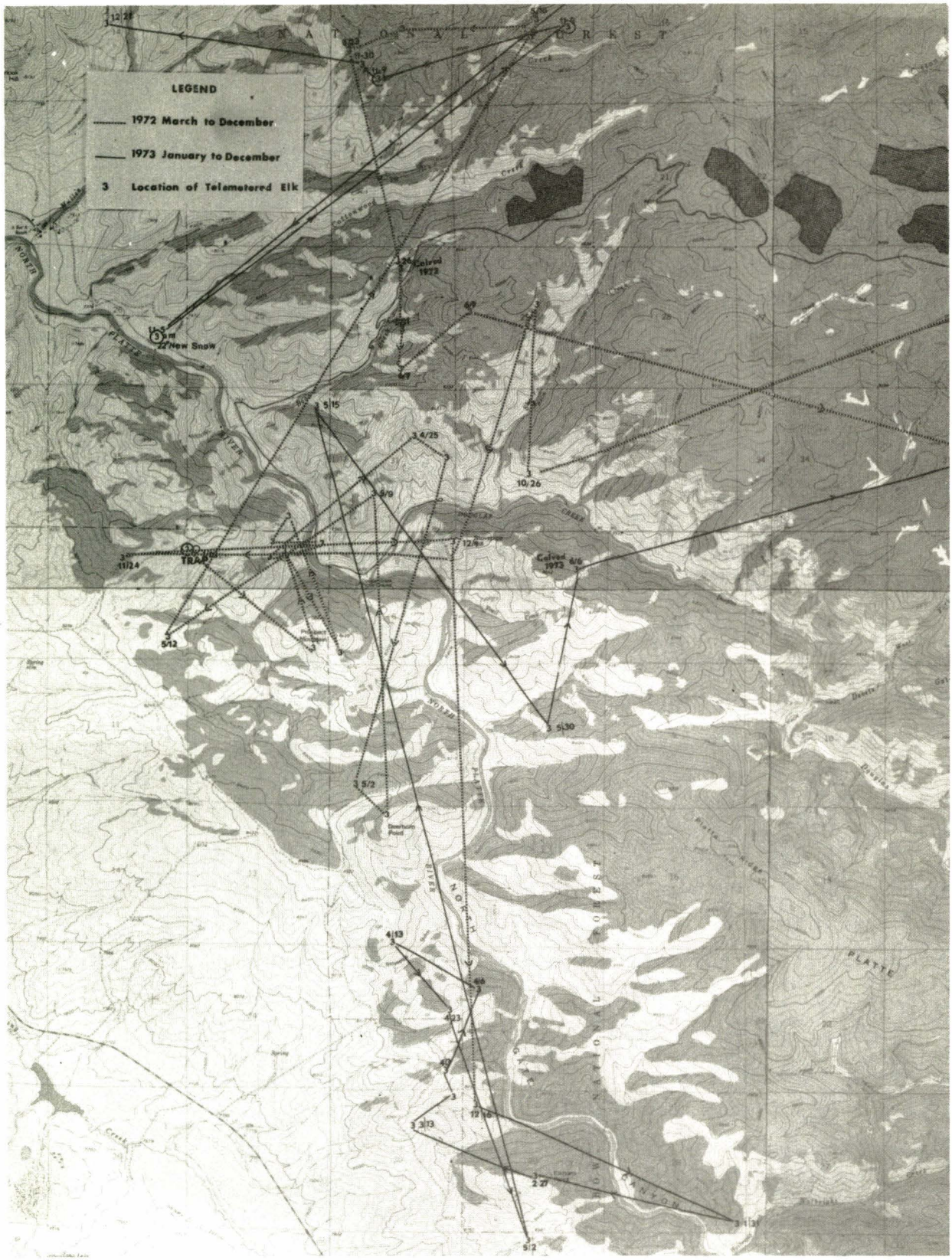

Fig. 24. Travels of telemetered cow number 3 during 21 months. Winter range travel is shown above, summer range travel is shown to the right.

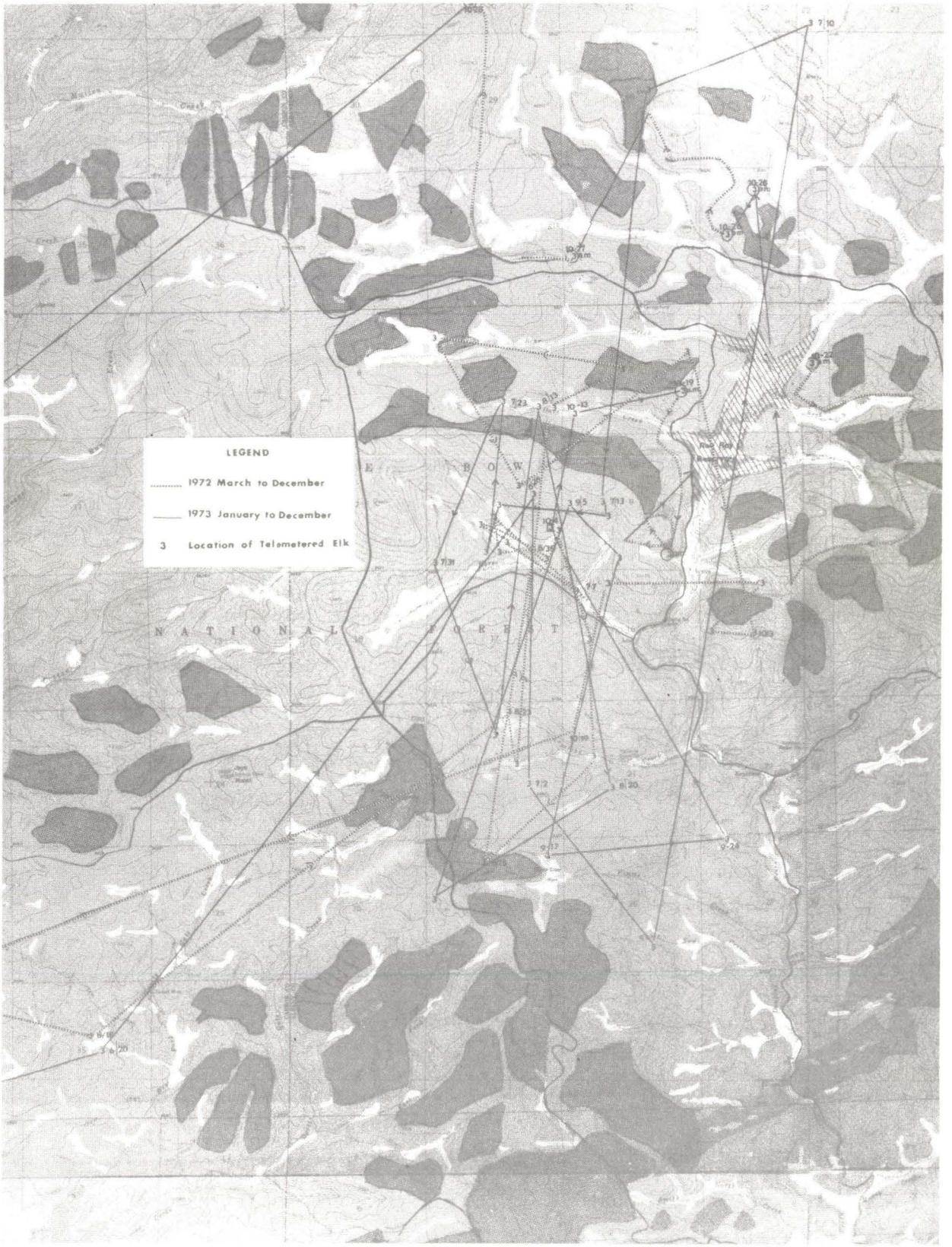

Fig. 24 (continued)

Vegetation

There are four major vegetation types on the elk winter range. The lower drainage bottoms are grassy meadows with some willow and aspen. They are narrow and restricted except for the hay meadows around the A-A Ranch. All of these areas are heavily grazed by livestock during the summer, and are often covered with snow in the winter. The most extensive type is the big sagebrush-antelope bitterbursh-grassland type found on ridges and southerly and westerly facing slopes. These areas are grazed by cattle in varying degrees during summer. Some of the more gentle slopes are extensively utilized while the steeper slopes are only lightly grazed or ungrazed. These areas hold the least amount of snow and the steep south facing slopes are bare of snow most of the winter. The aspen stands are not extensive and are found along bottoms and bordering the sagebrush-bitterbrush-grassland type at the upper elevations. Cattle graze the aspen stands quite extensively, and they usually have snow cover most of the winter. The conifers, either lodgepole pine (Pinus contorta) or Douglas fir (Pseudotsuga menziesii) are found on northerly facing slopes. There is very limited understory vegetation in this type and it is used very little by livestock, mostly for resting and rumination.

Transects to determine vegetation availability to elk on winter ranges were made on known heavily-used elk feeding sites within the big sagebrush-bitterbrush-grassland type. Most of these sites were located near the snow data transects on south-facing slopes. Data were taken in October before the elk arrived and in May when the elk were still present, but before plants had started growing. Transects were sampled in June when elk were present and plants were growing. The data in Table 21 show the predominance of browse, mainly big sagebrush and antelope bitterbrush, over all other plants all seasons of the year. Graminoids were next in abundance, with bluebunch wheatgrass, sedges, King's fescue, Idaho fescue, and Poa the major producers. The samples in April 1972 and June 1972-73 show the most forb cover. The two major species were sulfur wildbuckwheat (Eriogonum umbellatum) and

Table 21. Average percent of vegetation cover on winter elk feeding sites.[1]

Plants	June Green-growing	October Mature	May Mature
Graminoids	10.6	11.1	8.1
Carex sp.	2.4	2.9	0.5
Agropyron spicatum	4.9	7.0	6.3
Festuca idahoensis	0.2	0.2	1.3
Hesperochloa kingii	2.0	1.7	tr
Poa sp.	2.0	0.5	tr
Koeleria cristata	0.1	0.1	tr
Stipa comata	tr	0.1	tr
Other grasses	0.2	0.1	tr
Forbs	5.0	2.4	1.8
Chrysopsis villosa	1.2	1.0	0.2
Eriogonum umbellatum	0.5	1.0	0.3
Potentilla diversifolia	0.1	0.1	tr
Balsamorhiza sagittata	0.1	0.1	tr
Achillea lanulosa	0.1	tr	tr
Antennaria rosea	0.1	0.1	tr
Mertensia viridis	0.1		
Other forbs	2.0	0.1	0.1
Browse	27.2	30.0	27.9
Artemisia tridentata	10.6	11.0	13.3
Purshia tridentata	13.8	15.2	10.5
Amelanchier alnifolia	0.5	0.4	0.3
Artemisia frigida	0.1	0.2	0.2
Other browse	0.1	0.1	0.3

[1] See Appendix I for species authorities and common names.

hairy goldenaster (Chrysopsis villosa). Forbs were relatively scarce during the winter months.

Food Habits

Fresh elk fecal samples were collected from the winter ranges during the winters of 1967 through 1970. Examination of the 355 samples using microtechniques showed the elk winter diet to consist of 69 percent graminoids, 7 percent forbs, 13 percent sagebrush, and 11 percent other browse, Fig. 25. Fig. 25 shows that with increasing snow depth there is increased dependence by elk on grasses and sagebrush, and less dependence on forbs and other browse. This change in diet could be caused by animal preference or/and food availability. The elk go to the steeper and warmer south-facing slopes for food because they prefer to feed in areas of least snow depth and they eat dried grasses and sagebrush because they are the dominant palatable food plants on these sites. They do not have much choice.

The in vitro digestibility of three grass and four browse species collected from the elk winter range were reported by Ward (1971). Average digestion coefficients using inoculum from a wild elk were: grasses, 44.6 percent; antelope bitterbrush, 30.3 percent; big sagebrush, 53.0 percent; Saskatoon serviceberry, 34.6 percent; and red-osier dogwood, 37.3 percent.

Winter Elk Distribution

There was considerably more wind on the open ridges in 1972-73 compared to 1973-74 and considerably more wind on the open ridges than in the aspen or lodgepole pine stands. The large difference in amount of wind registered between the open ridge and the timber stands has a great effect on the chill factor.

The sharpest increase in wind chill occurs between 0 and 8 km per hour (kph). Average wind speeds on the open ridge were all greater than 13 kph while those in the trees were below one kph in 1972-73. Wind child factors (°F) were calculated for the different cover types using average minimum and maximum daily temperatures, average mph of

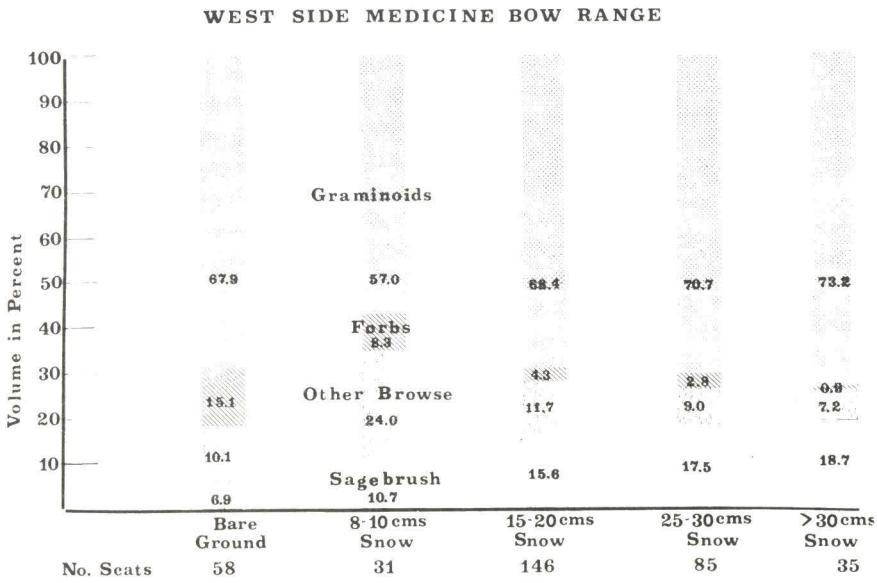

Fig. 25. Diet composition of elk on their winter range, based on scat analysis.

wind per month, and the FAA wind chill chart. The results are in Table 22.

Table 22. Average wind (mph) and wind chill factors in °F

	Lodgepole pine			Aspen			Open ridge		
Month	Average wind mph	Adjusted average wind chill temperature max.	min.	Average wind mph	Adjusted average wind chill temperature max.	min.	Average wind mph	Adjusted average wind chill temperature max.	min.
Nov.	0	28	9	0	32	14	13	15	-4
Dec.	0	25	3	0	34	9	14	24	-3
Jan.	0	23	1	0	27	7	13	19	-14
Feb.	0	27	3	0	32	7	10	27	-7
Mar.	0	30	9	0	34	10	16	16	-9
Apr.	0	34	18	0	39	23	16	30	1
May	0	48	27	----no records----			15	34	13

Observations indicated that elk were not influenced as much by temperature as they were the combination of wind and temperature. They were frequently seen feeding on very cold clear days, but were either in the timber or on the lee side of a hill during cold, windy weather. This is understandable when the wind chill factor is considered. Even though the temperature is lower on the north-facing slope in the pines, there is considerably less wind.

On a clear day with no wind the elk feeding on a south-facing slope would not only receive maximum radiation, but the temperature would be highest. There are some clear days when temperatures are well below freezing when elk move to timbered areas after feeding and resting in the open. Quite often on very cold, windy, clear days, elk are seen lying in the deep snow in the aspen. Conditions for low chill factor and good sun radiation would be about the best possible

for the animals' welfare at these sites, since considerable sunlight penetrates the open, leafless canopy.

1972. The winter of 1971-72 was the mildest observed on this range for the 1967-1974 period. Snow cover was very light below 2590 m where the elk stayed until the middle of May.

The elk trap was hauled by trailer and truck to the trap site at 2487 m and set up during December and January 1972. The trap was baited and set for the first time on February 4, 1972. Snow depths during this period were never greater than 20 cm and melted so there was never an accumulation on the south- or west-facing slopes. Snow stayed on the level ground for only two to three days after a storm. The trap was always accessible by four-wheel-drive vehicle, and the maximum snow depth was about 19 cm on February 28.

Elk were trapped on six different days during March and April 1972. Seven telemetered collars and 13 numbered collars were put on 17 cows and 3 female calves. Telemetry gear was put on only mature cows. The distribution of telemetered cow elk and their associates during the period of March-through-May 1972 is shown in Fig. 26. A great deal of the elk activity was centralized within two miles of the trap on the west side of the North Platte River. Snow depths were never considered a deterrent to elk movement during this period and the elk were frequently observed feeding on the snow-free sagebrush-bitterbrush-grassland slopes.

During the latter part of April and the first part of May all but one telemetered cow and her associates crossed the North Platte River to the east. All but the last cow and her associates crossed the river before the spring runoff. The last Cow 7 finally moved across the river between June 7 and 9. Cow 7 with her calf crossed the North Platte River and Douglas Creek during high water.

1973. The winter of 1972-73 was a heavy snow cover year on the winter elk range based on available past records, and was especially heavy compared to 1971-72. Snow came in early December and persisted even on level terrain until the latter part of April. Snow machines were necessary to reach the trap.

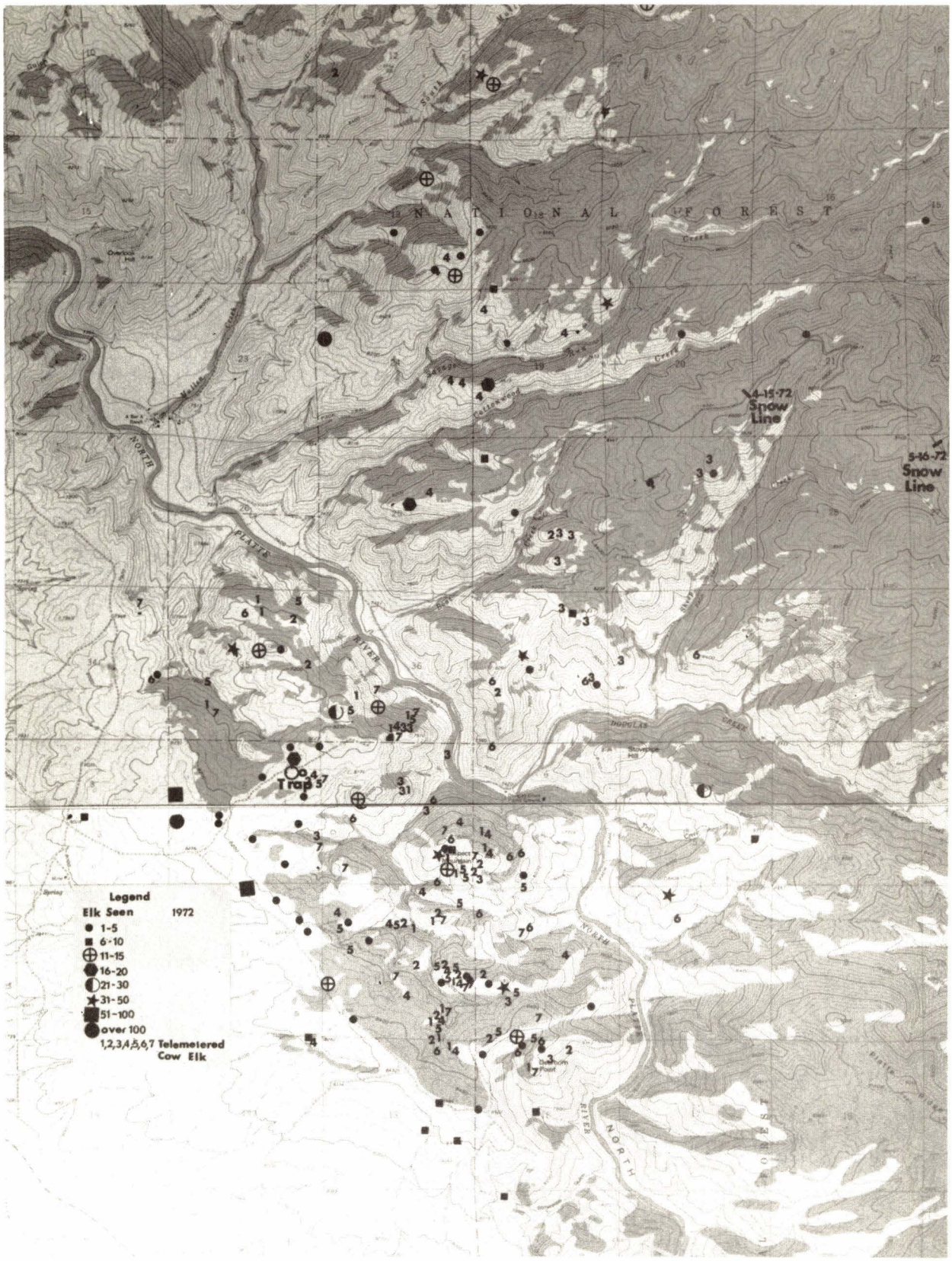

Fig. 26. Elk distribution during late winter, 1972.

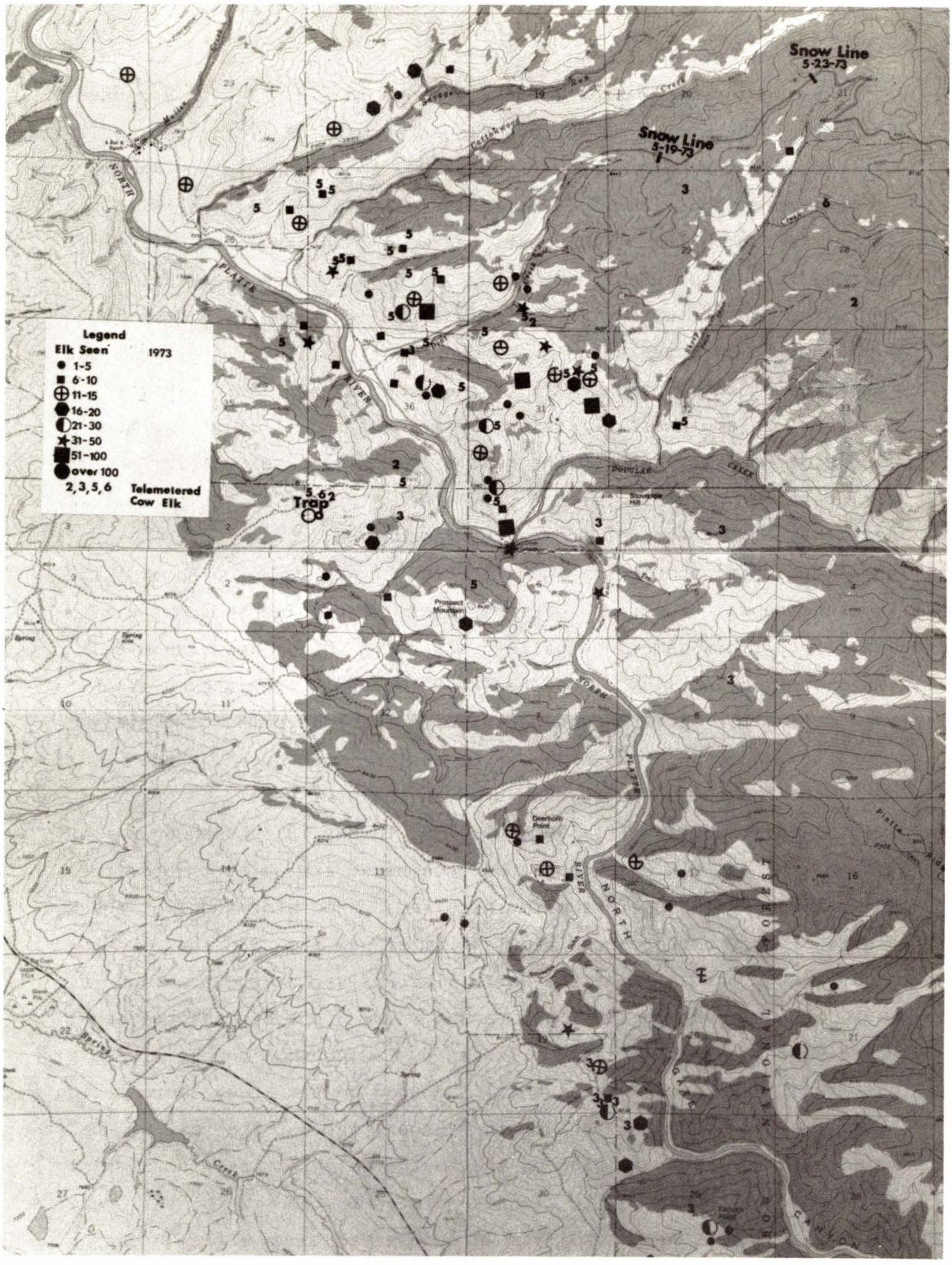

Fig. 27. Elk distribution during the winter of 1972-73.

The series of 12 snow transects shown in Fig. 22 were measured throughout the winter on various slopes within the winter elk habitat and produced the data shown in Table 23. Snow accumulation and water content were significantly greater on relatively level ground and slopes facing to the north, east, and west than on slopes over 42 percent facing southeast, south, or southwest. Snow accumulation and water content were significantly less in a stand of lodgepole pine than in an aspen stand or on open gentle slopes. Aspen did not reduce snow accumulation. All of the steep slopes facing in the southeast to southwest direction were free of snow from about the middle of February through the rest of the winter, except for short periods after major storms. A very steep slope (60%) facing directly south was almost free of snow after February 5.

The aerial photograph shown in Fig. 22 was taken on April 5, 1973 and shows the pattern of snow cover in relation to topography and cover. This same snow pattern was noted in the heavy snowfall years of 1968 and 1969 also, when there was good snow accumulation. Snow melt after April 23 was rapid, with the snow being completely gone first on open areas with a more southerly exposure. Snow persisted longest on north exposures in the pine trees.

Elk distribution from December 1972 to May 1973 is shown in Fig. 27. Eight elk were caught on December 6 and No. 5 transmitter and seven numbered collars were installed. Snow storms during the middle of December produced about 40 cm of new snow and the elk moved to the east side of the North Platte River at the trap and south up the river to the rough canyon. Cow 3 and her associates moved south, and Cow 5 east. Elk fed by pawing snow on the steep east- and west-facing slopes until the snow on the steep south-facing slopes melted off. From about mid-February through the rest of the winter elk were seen feeding on the south-facing slopes. Numbers of elk at each site were quite closely related to the size of the area. Elk with transmitters or collars were observed to move from one area to another, indicating interchange between groups, but the number of elk on each site stayed about the same.

Table 23. Snow and water measurements in centimeters on elk winter range, 1973.

Site No.	Place	Moisture	Jan. 12	Feb. 5	Mar. 13	Apr. 6	Apr. 23
1	Trap site	Snow	57.6±1.3	56.5±1.3	61.2±1.3	73.2±1.8	69.6±1.3
		Water	11.6±0.5	13.7±0.5	15.5±0.5	22.9±1.3	23.9±1.0
2	Aspen grove	Snow	53.6±1.5	65.0±1.0		79.2±1.0	82.0±1.5
		Water	10.9±0.2	16.5±0.5		23.4±0.8	27.7±0.8
3	Lodgepole pine	Snow	40.6±1.5	49.8±0.5	60.4±1.5	69.1±0.8	72.1±1.0
		Water	7.6±0.5	11.9±0.2	13.7±0.5	19.5±0.5	21.8±0.5
5	Lower camera site	Snow	21.1±2.0	32.0±0.5		0.0	0.0
		Water	3.3±1.5	8.6±0.5		0.0	0.0
6	Near beaver dam	Snow	40.1±0.5	31.8±1.0	10.2±2.8	0.0	0.0
		Water	5.6±0.8	8.1±0.5	4.6±1.3	0.0	0.0
7	West facing	Snow	46.5±1.5	40.9±0.8	Est. 41 cm	Est. 35 cm	Est. 15 cm
		Water	8.1±0.8	10.7±1.0			
8	Road along river	Snow	52.1±0.5	50.5±1.8	Est. 50 cm	Est. 35 cm	Est. 20 cm
		Water	10.2±0.5	12.7±0.5			
9	East facing	Snow	49.3±1.3	46.2±1.8	49.0±2.5	Est. 40 cm	Est. 40 cm
		Water	9.9±0.8	9.6±0.5	14.5±0.8		

Table 23. (continued)

Site No.	Place	Moisture	Jan. 12	Feb. 5	Mar. 13	Apr. 6	Apr. 23
11	Steep south slope	Snow		5.1±1.3	0.0	0.0	0.0
		Water		2.3±0.8	0.0	0.0	0.0
15*	Ridge top	Snow	21.4±3.0	64.0±3.0	66.8±2.5	82.3±2.8	83.0±2.3
		Water	4.3±0.5	18.3±1.3	17.3±1.0	30.0±0.8	29.0±1.0
16*	Deerhorn Point	Snow		60.7±1.0		78.7±0.5	Est. 79 cm
		Water		19.0±1.0		24.4±0.5	
17*	Highway 230	Snow	45.0±2.0			44.4±1.3	Est. 25 cm
		Water	7.1±0.5			15.2±1.0	

*Sites not shown on aerial photo, Fig. 22.

A total of 551 elk, 19 bighorn sheep, and 11 mule deer were counted on April 13, just eight days after the aerial photo of snow distribution was made. Elk distribution in relation to snow distribution is shown in Fig. 22 for a portion of the study area near the elk trap. All of the elk and sheep were on snow-free, southerly-facing slopes. The sheep had stayed in the area all winter and used the same areas as the elk for feeding sites. All of the mule deer were observed in the steep canyon south of the elk trap, 4 on the west side of the river and 7 on the east, and were also on steep, south-facing slopes in close proximity to elk.

1974. During the winter of 1973-74, snow measurements were made on six sites on three different dates (Table 24). Snow accumulation on the elk winter range was about 50 percent of that recorded in 1972-73, but elk distribution was quite similar to the winter with deeper snow. The elk stayed on the east side of the North Platte River and were again seen feeding on the snow-free, south-facing slopes when the census was made on April 15, 1974.

Spring Migration

As the snow melts in the spring, the snow line moves higher in elevation. By the end of May and the first part of June, which is the elk calving season, the snow line on the study area was above 2743 m. Most of the elk stayed at least 1.6 km below the snow line where the vegetation is growing fast and food is plentiful.

One of the telemetered cows and a couple of her associates moved above the snow line on May 26, 1972. Four days later she was located back downhill where the vegetation was green. There was some bare ground beginning to appear in the open parks at the higher elevations, but no green-growing vegetation was observed. Evidently elk make exploratory trips to these higher parks early in the spring and return to the lower sites when they find no green food.

The elk scatter over the range between 2560 to 2743 m elevation during the calving season. Very few calves are born within close proximity of snow, unless there is an unusually late snow storm such

Table 24. Snow depths and water content (cm) at various sites within elk winter range along the North Platte River, 1974.

Site No.	Place	Moisture	Feb. 11	Mar. 18	Apr. 1
11	Steep south slope	Snow	0.0	0.0	0.0
		Water	0.0	0.0	0.0
7	West facing slope	Snow	37.8±1.0	37.1±8.6	13.7±3.0
		Water	11.4±0.8	8.1±1.5	4.1±1.3
8	Road along river	Snow	38.9±0.5	43.4±1.3	29.7±0.5
		Water	12.2±1.0	8.1±1.0	8.9±0.2
5	Lower camera site	Snow	20.8±1.3	*	*
		Water	7.6±0.5	*	*
6	Near beaver dam	Snow	17.3±1.3	*	*
		Water	8.1±1.5	*	*
10	Mouth of Douglas Creek	Snow	0.0	0.0	0.0
		Water	0.0	0.0	0.0

*No measurements taken.

as that on June 9, 1974. This particular late storm did not move the elk. Deep snow and extended periods of cold weather in the spring could cause calf losses.

Old winter snow goes through three stages as it melts in the higher country. It is very hard and coarse-grained at the beginning of the spring period. As it melts, the upper surface gets wet and soft and the bottom layer starts to melt. As long as the weather remains cold and the depth stays about 60 cm, the snow is still hard enough to support an elk, man, or vehicle. On warm afternoons, snow depths of 30 cm get too soft to support elk. As the snow melts, it becomes even softer and will not support a man. All these stages can be encountered on a warm afternoon in June when going uphill on a road or going from an open wind-swept park into the timber at the higher elevations.

Snow densities in the timber at 3048 m elevation on July 4, 1974 averaged 55 with a range of 58 (79 cm of snow with 46 cm of water) to 40 (25 cm of snow with 10 cm of water). An adult elk had made tracks about 2.5 cm deep across the snow where the measurements were taken. A jeep was driven over a 152 cm-deep snowdrift at about the same elevation on July 4, 1973. These conditions allow elk to travel on top of deep snow through the timber to get to open parks or meadows at higher elevations. They do not have to move through soft heavy snow except along the edges where it is less than 30 cm thick.

Discussion

Snow cover has a definite effect on elk. The depth and physical characteristics of the snow determine the distribution, movements, and feeding habits of elk on their range. Winter and early spring is the most critical time. During the winter the depths and density of snow cover on elk winter range are highly variable from one year to the next and even during each winter. Under light snow conditions there are few problems and the elk move considerably using all of the area with no particular preference except to feed

where the food is plentiful and to stay in the timber when a cold wind exists. During a winter of heavy snow and cold temperatures the elk were able to paw through 46 cm of light new snow in December and January to obtain food. Their most favored areas during this time were steep east- and west-facing slopes where there were good food supplies and cattle had not grazed. By the middle of February and continuing through to spring the snow on the steep, southerly-facing slopes melted off, due to the increased amounts of solar energy. The elk were seen feeding on these areas. The number of elk associated with a snow-free area was usually related to the size of the area. There was movement between elk groups, but numbers did not change appreciably. The elk retreated to the timbered areas during periods of cold, windy weather where the wind chill factor was greatly reduced.

Elk winter range during a heavy snow year was below 2743 m. A weather modification program to increase snow depths above this level would not affect elk on their winter range. Since elk calving areas are below this level, it is doubtful if there would be problems created. Work reported by Leaf and Brink (1972) and Haeffner and Leaf (1973) suggests that winter snow accumulation higher than normal apparently does not delay the disappearance of the last snow. Therefore, snow accumulations at the higher elevations would not affect elk on the summer range unless they came very early in the fall.

Increased snow accumulations on elk range below 2743 m would have some detrimental effects, particularly if they came early in the season when predictions of future accumulations is unknown, or during the calving season.

How severe the effects of snow on elk would be on winter range are dependent upon many factors. Two good examples of the extremes were evident within 40 km of each other in the North Platte River valley during January to April 1973. On our study area the elk came through the heavy snow period by utilizing food available on the bare, steep, south slopes in the rough canyon country. An area about

40 km north and just east of Saratoga, Wyoming had sufficiently deep snow cover that an elk feeding program was conducted to keep the elk from either starving or raiding rancher's haystacks. Most of the area where the elk were herded to be fed alfalfa hay was purchased by the Wyoming Game and Fish Commission for use as a winter elk range. The elevation ranges from 2134 to about 2530 m with mostly gentle, west slopes. Early snows melted, then froze, forming ice at ground level. Further snow storms and cold temperatures made food very difficult to obtain even when the animals pawed through the snow. Snow depths were not considered to be excessive (mostly below 50 cm), but the physical characteristics of the snow cover made it impossible for the elk to get enough food. The feeding program was initiated when the elk started to lose weight and began to utilize ranchers' haystacks.

The effects of snow depths on elk cannot be generalized for all winter ranges. Each location of elk winter range has considerable variation in topography, vegetation, and climate. It is apparent that animals have more difficulty surviving during cold, heavy-snow-depth winters. Results from this study would indicate that target areas for increased snow accumulation through weather modification programs should be above the upper limits of the elk winter range (about 2620 m for this study area) and that an additional 15 to 30 percent of snow at higher elevations would have no adverse effects on elk.

We have seen elk and their calves crossing streams at flood stage, and have no basis for suggesting increased mortality due to increased run-off from cloud-seeding.

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THE IMPACT OF SNOW ON MULE DEER

M. D. Strickland and K. Diem

There is a paucity of information on the response of mule deer to snow accumulation. Gilbert et al. (1970) suggested that deer movements were hindered by snow, and found that during heavy-snow winters in Middle Park, Colorado, the availability of food was reduced sufficiently to severely limit the carrying capacity of the range. Indeed, the limiting factor for many mule deer populations in the Rocky Mountains is available winter range. Deer die-offs of considerable magnitude occur in severe weather, and winter weather modification producing more snow could have a serious effect on mule deer survival. With this in mind, an intensive study of the mule deer inhabiting the Medicine Bow Mountains was initiated in the summer of 1972, the major objectives and study area being the same as those listed for the elk study (p. 105).

Methods and Materials

Deer distribution on the winter range was determined by traveling survey routes by automobile, snowmachine and on foot. In addition, numerous flights were made with fixed-wing aircraft. Movements, distribution and home-range of individual animals were ascertained by observations of marked animals and by monitoring radio-tagged animals.

Deer were captured on the summer range and intermediate ranges using a capture gun (Pneu-dart, Williamsburg, Pa.) and the drug sucostrine. The dosage rate was 0.05 mg/lb body weight using liquid sucostrine (Pearson, Smith and Urness 1963). However, when

powdered sucostrine was used a dosage rate of 0.1 mg/lb was required. Deer were captured on the winter range by trapping with the modified Clover single-gate deer trap (Clover 1956). Alfalfa proved to be the most efficient bait.

Individual animals were marked with vinyl-coated canvas collars individualized with a combination colored symbol-number system. Each deer was also marked with a Wyoming Game and Fish Department metal ear tag. Nine deer were fitted with a high frequency (172 mhz) radio transmitter mounted on a collar. Radio-tagged deer were monitored from the ground using a yagi directional antenna and from aircraft using two whip antennas mounted on the center of the plane. Radios and collars were built by the Electrical Engineering Department, University of Wyoming and by Jerry Cupal, Rocky Mountain Forest and Range Experiment Station, the U. S. Forest Service, Laramie, Wyoming. Receivers used included a Drake tuneable receiver and a Telonics portable crystal operated receiver.

Herd composition and age structure were determined for deer on both summer and winter ranges. Animals observed on survey routes and from random observations were classified as to sex and age group (i.e. fawn, yearling or adult). Teeth were collected from animals taken during hunting seasons and from dead animals encountered in field work. The ages of these animals were determined by counting cementum anuli (Low and Cowan 1963), using the technique described for badgers by Crowe and Strickland (1974). Animals captured during the course of the study were aged by tooth replacement and wear.

A population estimate was made for each year based on the pre- and post-hunt sex ratios, using the relationships discussed by Rasmussen and Doman (1943). An estimate of herd productivity was made following the technique described by Hanson (1963).

Snow measurements were taken at various locations over the intermediate and winter deer ranges. Snow characteristics and mule deer activity were monitored by time-lapse photography. In addition, randomly chosen feeding and non-feeding sites were evaluated as to

winter snow conditions and mule deer use. Measurements included snow depth, water content, percent slope and aspect. A map of snow distribution at various dates during the two winters was compiled using photographs taken from the Earth Resources Technology Satelite (ERTS). Images taken in Band 7 were found to provide the best information on snow distribution. An outline of snow cover was transferred to a base map with the use of positive transparancies and a Bausch and Lomb-Zoom Transfer Scope. Each observation of deer on the winter range was accompanied by an estimate of snow depth.

Relative use of habitat types was evaluated by direct observation and pellet group counts (Neff 1968). In the spring of 1973 vegetation measurements and pellet group counts were made on three sites in the Beaver Hills area that were judged to be in different availability categories due to snow cover. The following spring, measurements were made again on Beaver Hills and two additional areas, Baggott Rocks and Bennett Peak. Shrub composition on these areas was determined by the line intercept method (Canfield 1941). Condition and utilization measurements of key browse species within key range areas were made by utilizing the range survey technique described by Cole (1963). This technique was found to be unsatisfactory for sagebrush. Criteria for measuring condition and utilization of sagebrush were developed during the study and are indicated on tables where data are presented. Pellet transects, using 300 plots (each $4m^2$), were established through each area, the plots being located at 15 m intervals. Data from vegetation measurements and pellet group counts made on the study area since 1959 by the Wyoming Game and Fish Department and the U. S. Forest Service were also utilized. Plant species, with the exception of sagebrush, were named according to Harrington (1954). Beetle and Young (1956) was used for sagebrush nomenclature.

Winter food habits were determined primarily from microscopic examination of fecal samples (Ward 1970). In addition, an attempt was made to identify plant species utilized by deer observed feeding. The nutritional quality of forage species important in the mule deer

diet during the winter were determined by an acid detergent analysis (Van Soest 1966). The dry matter digestibility (DMD) of these forage species was determined by the two-stage *in vitro* technique described by Tilley and Terry (1963). Rumen fluid for the digestibility trials was collected from animals sacrified on the study area during March and April by the Wyoming Game and Fish Department.

A concentrated effort was made to locate winter-killed animals. When located their nutritional condition at the time of death was judged by examining femoral bone marrow (Cheatum 1949).

The relationship of winter precipitation and temperature to fluctuations of spring pellet group counts was examined by multiple regression analysis.

Results

The mule deer herd inhabiting the study area was composed of sedentary and migratory segments. The sedentary segment of the herd inhabited the lower elevations (2133 to 2438 m) throughout the year with little seasonal movement. The migratory segment wintered below 2438 m and summered on ranges between 2590 and 3048 m. During the periods of rut in the fall and fawning in the spring the migratory animals occupied an intermediate range (2438 to 2743 m).

The vegetation on the summer range is characterized by large stands of lodgepole pine. Smaller stands of Engelmann spruce and subalpine fir occur on cooler more mesic sites below 3048 m and extend above 3048 m in continuous stands to timberline (approximately 3291 m). The dense stands of conifers are interspersed with willow bogs and subalpine meadows and numerous clearcuts in some areas.

The vegetation on the intermediate range is typically an *Artemisia-Agropyron* association dominated by mountain big sagebrush (*Artemisia tridentata vaseyana*), antelope bitterbrush (*Purshia tridentata*) and bluebunch wheat grass (*Agropyron spicatum*). Aspen (*Populus tremuloides*) is abundant at lower timberline.

The winter range is characterized by an *Artemisia-Agropyron* association and an *Artemisia-Juniperus* association in rocky areas

below 2590 m. The dominants of the latter association include Wyoming big sagebrush (Artemisia tridentata wyomingensis), black sagebrush (Artemisia nova), rabbitbrush (Chrysothamnus spp.), antelope bitterbrush and juniper (Juniperus scopulorum). Wyoming big sagebrush is replaced by mountain big sagebrush above 2438 m.

During the periods of greatest snow cover, the majority of the deer occupy three critical wintering areas--Beaver Hills, Bennett Peak and Baggott Rocks (Fig. 28).

Beaver Hills

Beaver Hills is a southeast to northwest line of hills ranging in elevation from 2499 m on the south to 2225 m on the north end. The south end of the Hills are characterized by steep ridges covered with an Artemisia-Agropyron association. The north end is characterized by numerous rock outcroppings with an attendant Artemisia-Juniperus association. This area has one of the greatest concentrations of Wyoming big sagebrush in Wyoming (Beetle person. comm.), which is the dominant browse species in the area (Table 25). This subspecies is the most palatable form of big sagebrush (Hanks et al. 1971). Browse species increased in percent cover in 1974 with a concomittant decrease in bareground.

Bennett Peak

The Bennett Peak wintering area is located along the North Platte River. West of the river the area is dominated by a main peak, rising from 2194 m at the base to 2529 m at the highest point. Numerous lesser peaks are located to the east of the river. All of the peaks are covered with large boulders and are very steep in character. The southern, southeastern and southwestern slopes are covered with an Artemisia-Juniperus association. The north facing slopes are covered with dense stands of Douglas fir (Pseudotsuga menziesii) with understory of antelope bitterbursh and squaw currant (Ribes cereum). Numerous open sites on the north facing slopes have decadent stands of

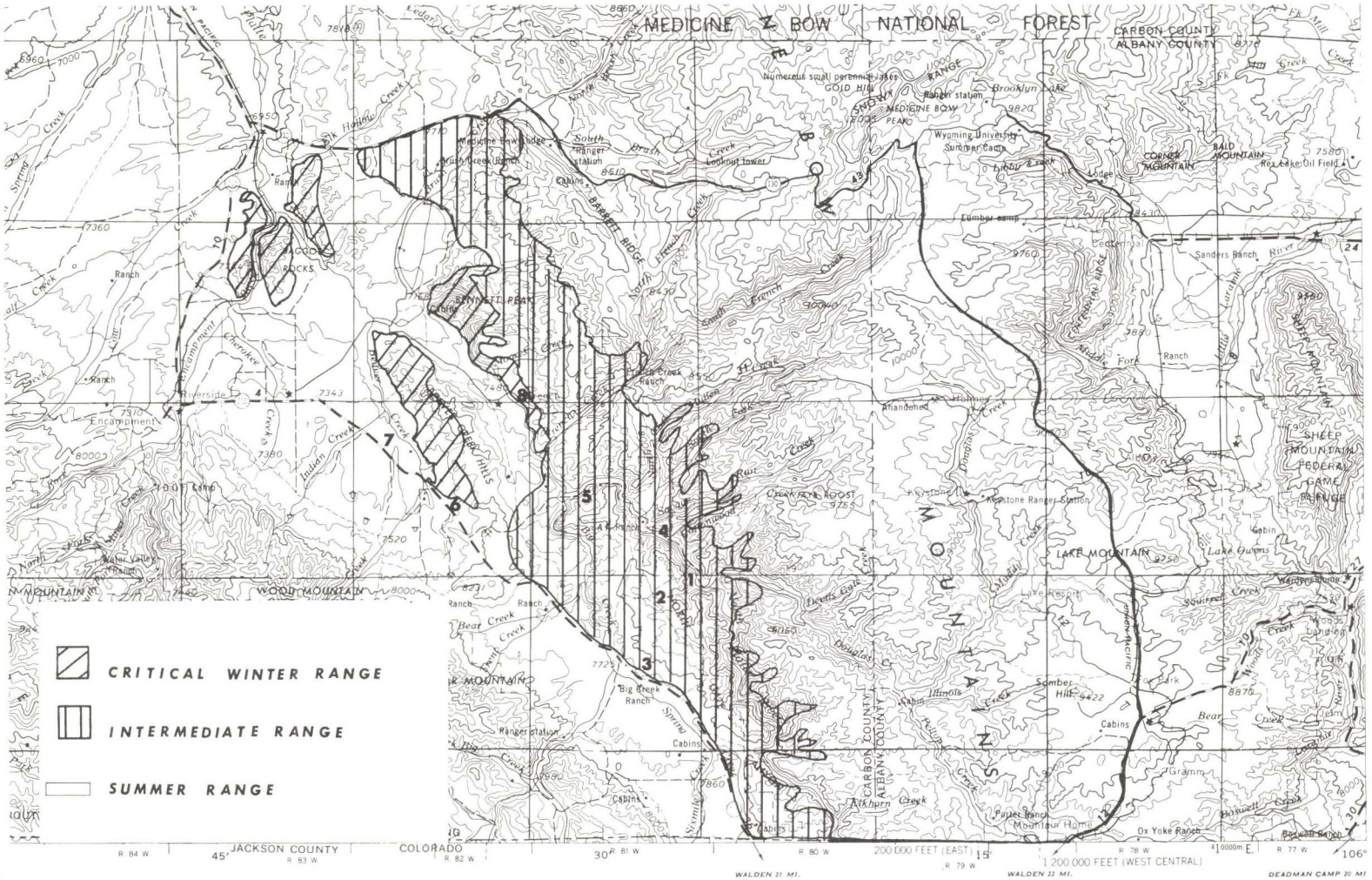

Fig. 28. Seasonal ranges of the mule deer herd on the Snowy Range study area. Numbers indicate the location of sites where permanent snow transects were established. The sites are: 1. Deer slope, 2. trap site, 3. Big Creek Ranch, 4. Cottonwood Creek, 5. Big Creek, 6. No Name Creek, 7. Antelope Creek, and 8. Sanger Ranch.

Table 25. Species composition and dominance of browse plants on three different winter availability sites[1] on the Beaver Hills wintering area in 1973 and 1974.

Species[2]	1973			1974			Difference		
	Site A[1]	Site B	Site C	Site A	Site B	Site C	Site A	Site B	Site C
Bare ground	62.8	62.9	71.3	59.0	59.4	64.9	+3.8	+3.5	+6.4
Artemisia tridentata	20.0	12.3	9.0	26.1	15.7	13.5	+6.1	+3.4	+4.5
A. frigida		0.4	0.5	0	0.8	0.4	0.0	+0.4	-0.1
Chrysothamnus viscidiflorus	0.0	0.7	0.0	0.4	1.6	0.3	+0.4	+0.9	+0.3
C. nauseosus	0.3	0.0	0.1	0.0	0.0	0.0	+0.3	0.0	+0.1
Purshia tridentata	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	+0.3
Opuntia polyacantha	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	+0.2
Ceanothus sp.	0.0	0.0	0.5	1.0	0.0	0.8	-1.0	0.0	+0.3
Grass and forbs	16.9	23.7	18.6	13.5	22.5	19.9	-3.4	-1.2	-1.3

[1] A = Unavailable due to winter snow cover
B = Available during part of the winter
C = Available the entire winter

[2] See Appendix I for species authorities and common names.

mountain mahogany (Cercocarpus montanus). Aspen occurs at sites where springs or seeps occur and around water holes. Browse transects indicate a very low shrub cover on the critical wintering area on Bennett Peak (Table 26). This shrub component is better represented in the stand near the base of the peak and the sagebrush flat surrounding the peak.

Baggott Rocks

The Baggott Rocks area is located at the northwestern end of the study area along the Encampment and North Platte Rivers. The area is characterized by steep rocky hills and ranges in elevation from 2133 m at the base to 2360 m at the highest point. The vegetation is an Artemisia-Juniperus association. Sagebrush is the dominant shrub species comprising 24 percent of the cover in the rocks and 16 percent of the cover in the surrounding sagebrush flats (Table 26). Mountain mahogany is abundant on the north exposures, however, all stands examined during the study were decadent. Decadent squaw currant (Ribes sp.) plants also occur in isolated areas. Most mountain mahogany and currant plants encountered in the spring of 1974 were heavily infested by tent caterpillars.

The terrain between the three areas is characterized by rolling hills mostly in cultivation for winter wheat. Areas not in cultivation are covered with Wyoming big sagebrush and black sagebrush. Year round cattle grazing occurs on most private lands in this area. Summer grazing on public land in the Beaver Hills and Bennett Peak area also occurs. The Baggott Rocks area was grazed in 1973 but not in 1974. Antelope used this area for both summer and winter range.

The sedentary segment of the deer herd occupy the above three areas as well as areas extending further south along the North Platte River in the North Gate Canyon. This area is vegetated with the Artemisia-Juniperus association. However, mountain big sagebrush and antelope bitterbursh are the dominant shrubs; Wyoming big sagebrush and black sagebrush are rare. Limber pine (Pinus flexilis), Douglas fir and service-berry (Amelanchier alnifolia) are also abundant.

Table 26. Species composition and dominance of browse plants on the Bennett Peak and Baggott Rocks wintering areas[1] in 1974.

Species[2]	Bennett Peak A[1]	Bennett Peak B	Bennett Peak C	Baggott Rocks A	Baggott Rocks C
Bare ground	26.9	7.3	47.4	60.4	65.8
Artemisia tridentata	4.8	6.2	0.9	24.3	15.6
A. frigida	2.1	0.0	0.0	0.0	0.0
Chrysothamnus nauseosus	6.3	1.0	0.3	0.0	0.3
C. viscidiflorus	11.6	1.4	0.0	0.0	1.2
Opuntia polyacantha	11.4	0.4	0.2	0.1	0.1
Purshia tridentata	0.0	20.8	2.2	0.0	1.6
Juniperus scopulorum	0.0	0.0	0.0	0.0	3.3
Grass and forbs	37.9	62.9	49.0	15.3	12.1

[1]A = Available from early March through spring
B = Available from late February through spring
C = Critical winter range

[2]See Appendix I for species authorities and common names.

Fall Migration in Relation to Snow Accumulation

The initiation of the fall migration occurred during the first 2 weeks in October, 1972 and 1973. Few deer were seen on the summer range after the third week in October in either year. Two adult does outfitted with radio transmitters, deer 3 and 4, in the summer of 1972 were last located on the summer range on September 29. The next location was on the intermediate range on October 6, at elevations of 2377 and 2407 m, respectively (Fig. 29). This was a movement of approximately 24 km for deer 3 and 26 km for deer 4. Two light snowfalls occurred prior to the movement of the deer, yet, no snow was on the ground at the time of the movement. No snow occurred on the summer range prior to the fall migration in 1973. In the fall of 1973, deer 4 was last seen on the summer range on October 22. It is not known when she migrated but no snow fell prior to November 1.

Rut was observed on the intermediate range during the last week in October and first week in November in both years. Breeding behavior continued throughout the month of November.

The winter of 1972-1973 was extremely severe. Deep snow accumulated on the intermediate range by late December and persisted through early April in some areas (Table 27). By the second week in January most of the deer were on the critical wintering areas. Snow measurements made at three deer feeding sites on the intermediate range immediately after this movement showed depths of 40 cm, 58 cm and 45 cm of crusted snow. No deer were seen at these sites the remainder of the winter.

In the winter of 1973-1974 the deer remained on the intermediate range until the first of February. Snow depths in 1974 reached their maximum in mid-February (Table 28), but did not persist as did the deep snows of the previous year.

Deep snow also accumulated on much of the mule deer winter range during both winters. Snow distribution at various times during the two winters are illustrated in Figure 30. On January 30, 1974 approximately 64.1 km^2 were without heavy snow cover. In 1974 at about

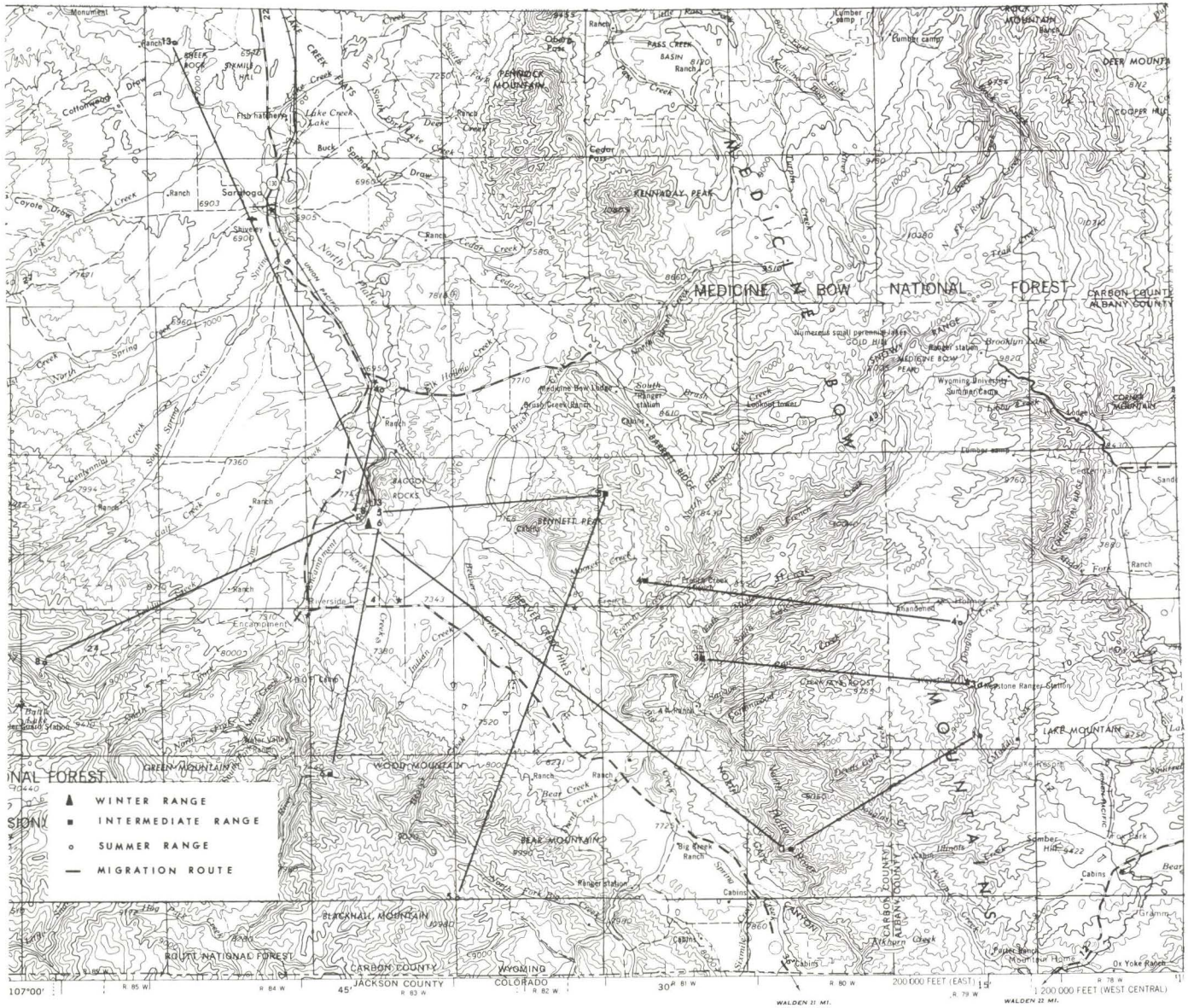

Fig. 29. Dispersal of telemetered deer from the summer range in the fall of 1972 (3 and 4') and dispersal of telemetered and collared deer from the winter range in the spring of 1974.

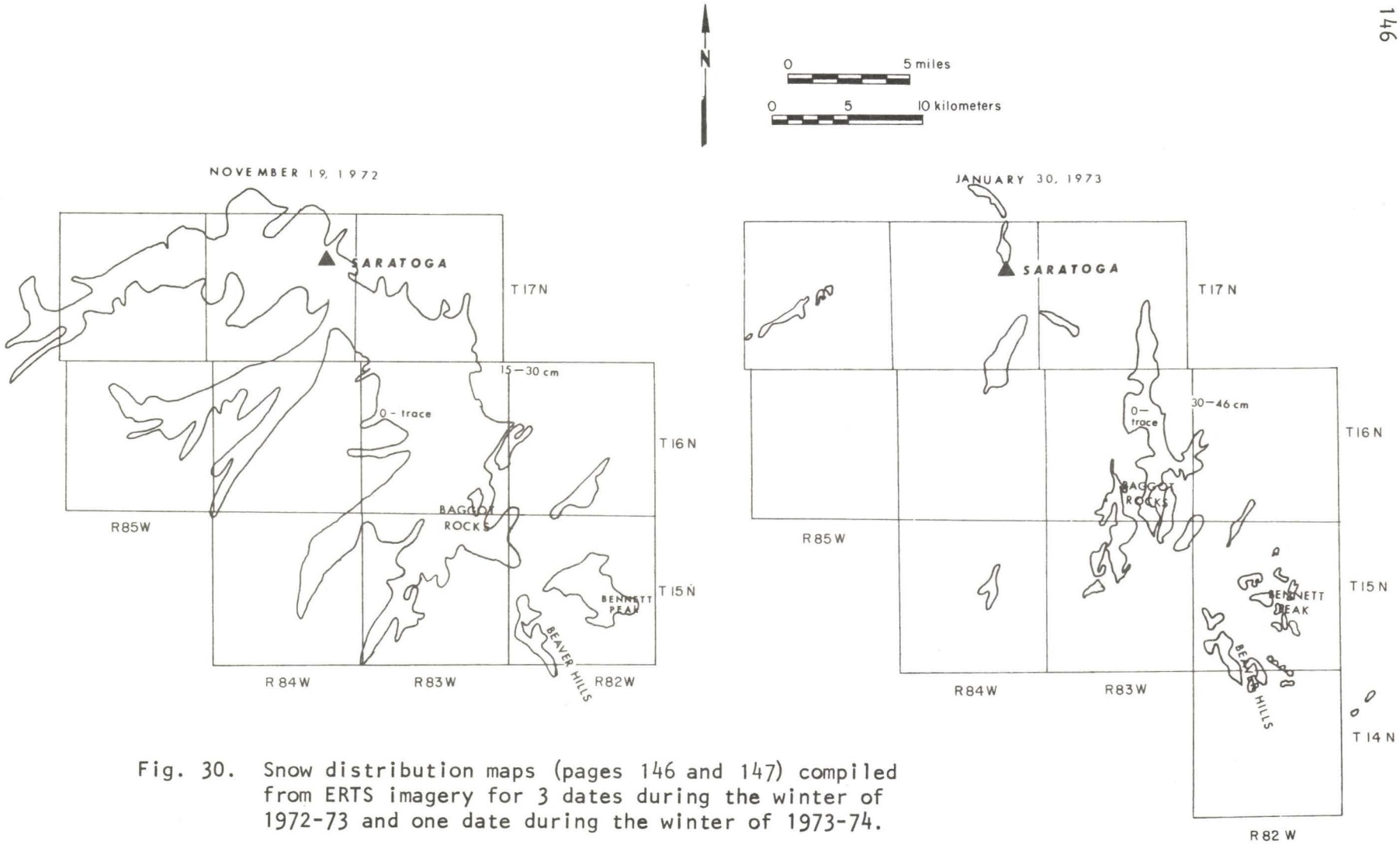

Fig. 30. Snow distribution maps (pages 146 and 147) compiled from ERTS imagery for 3 dates during the winter of 1972-73 and one date during the winter of 1973-74.

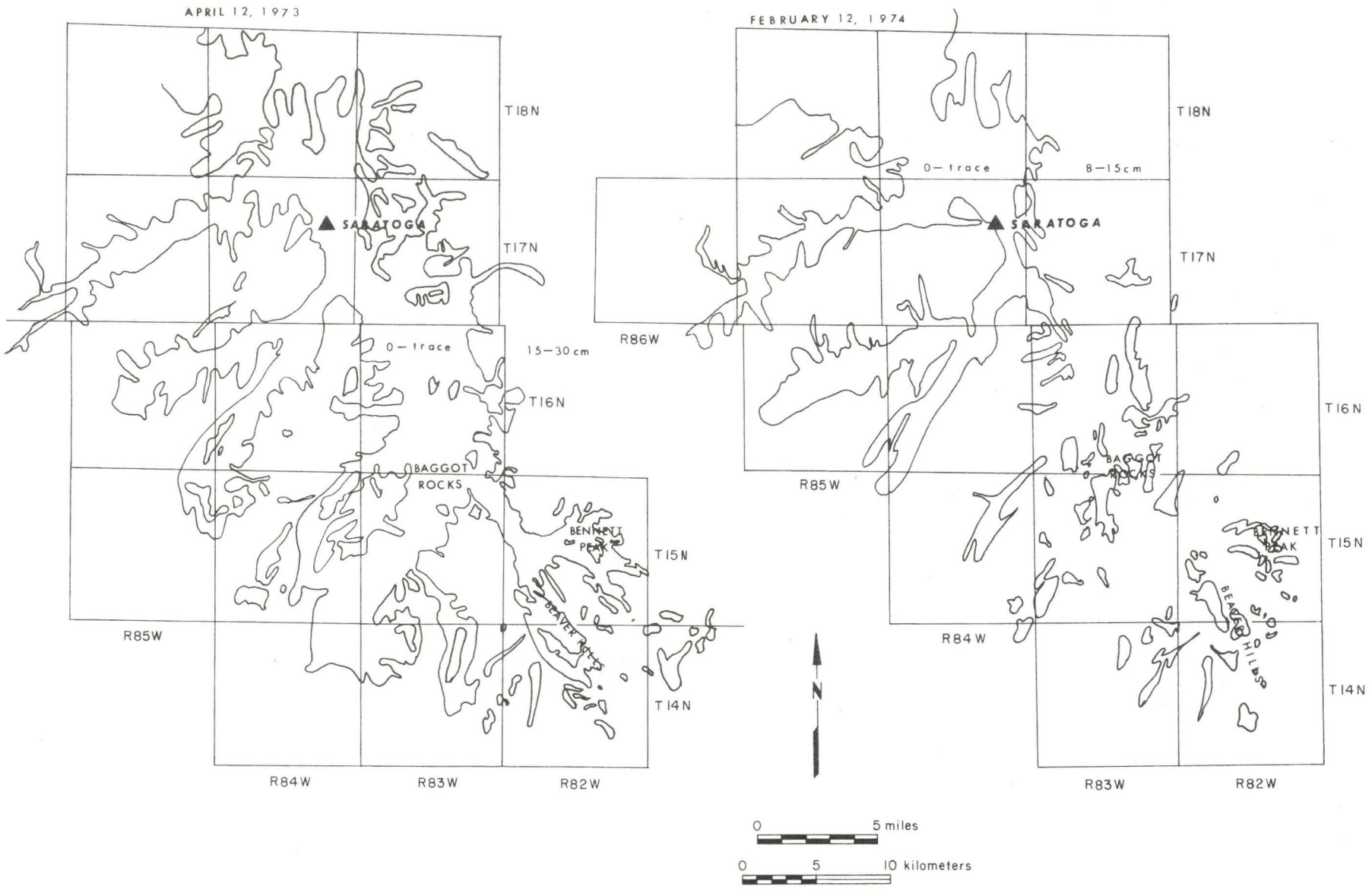
APRIL 12, 1973
T18N
SARATOGA
T17N
0—trace
15—30 cm
T16N
BAGGOT ROCKS
BENNETT PEAK
T15N
BEAVER CREEK
R85W
T14N
R84W
R83W
R82W
FEBRUARY 12, 1974
T18N
0—trace
8—15cm
SARATOGA
T17N
R86W
T16N
BAGGOT ROCKS
R85W
BENNETT PEAK
T15N
BEAVER CREEK
R84W
T14N
R83W
R82W
N
0 5 miles
0 5 10 kilometers

Table 27. Snow depths, water content and the standard error of the mean for the measurements at various deer feeding and non-feeding sites on mule deer winter range in 1973.

Site	Aspect	Percent Slope	Jan. 3				Jan. 15				Feb. 5			
			snow depth(cm)	SE	water depth(cm)	SE	snow depth(cm)	SE	water depth(cm)	SE	snow depth(cm)	SE	water depth(cm)	SE
Intermediate Range														
Deer Slope	S	42												
Trap Site	WSW	12	57.7	0.5	11.7	0.2	*		*		56.6	0.5	13.7	0.2
Big Creek Ranch	SW	8	45.0	0.8	7.1	0.2	*		*		*		*	
Cottonwood Creek	SW	39	*		*		*		*		*		*	
Big Creek	NE	8	*		*		*		*		*		*	
Winter Range														
Antelope Creek	NW	8	*		*		37.3	0.8	10.4	0.6	*		*	
No Name Creek	SW	8	*		*		*		*		16.3	0.5	7.4	0.2

Site	Aspect	Percent Slope	Feb. 17				Mar. 13			
			snow depth(cm)	SE	water depth(cm)	SE	snow depth(cm)	SE	water depth(cm)	SE
Intermediate Range										
Deer Slope	S	42	*		*		*		*	
Trap Site	WSW	12	*		*		*		*	
Big Creek Ranch	SW	8	*		*		*		*	
Cottonwood Creek	SW	39	60.0	1.2	12.7	0.3	*		*	
Big Creek	NE	8	59.4	6.1	15.5	0.2	*		*	
Winter Range										
Antelope Creek	NW	8	*		*		*		*	
No Name Creek	SW	8	*		*		*		*	

* No measurements taken

Table 27. (Continued)

Site	Aspect	Percent Slope	Apr. 6				Apr.23			
			snow		water		snow		water	
Intermediate Range			depth(cm)	SE	depth(cm)	SE	depth(cm)	SE	depth(cm)	SE
Deer Slope	S	42	0.0		0.0		0.0		0.0	
Trap Site	WSW	12	73.2	0.7	22.9	0.5	69.6	0.5	23.9	0.4
Big Creek Ranch	SW	8	44.5	0.5	15.2	0.4				
Cottonwood Creek	SW	39	*		*		*		*	
Big Creek	NE	8	*		*		*		*	
Winter Range										
Antelope Creek	NW	8	*		*		*		*	
No Name Creek	SW	8	*		*		*		*	

* No measurements taken

Table 28. Snow depths, water content and the standard error of the mean for the measurements at various deer feeding and non-feeding sites on mule deer winter range in 1973.

Site	Aspect	Percent Slope	Feb. 13				Mar. 8				Apr. 5			
			snow		water		snow		water		snow		water	
			depth(cm)	SE	depth(cm)	SE	depth(cm)	SE	depth(cm)	SE	depth(cm)	SE	depth(cm)	SE
Intermediate Range														
Big Creek Ranch	SW	8	38.6	0.3	8.4	0.3	23.4	0.5	6.6	0.3	11.2	0.3	3.6	0.1
Big Creek	NE	8	40.6	1.2	8.4	0.4	37.0	1.0	7.9	1.0	18.3	2.0	4.6	0.7
Deer Slope	S	42	17.3	0.5	8.1	0.6	*		*		*		*	
Winter Range														
Sanger Ranch	SW	13	25.7	0.7	6.4	0.4	0.0		0.0		0.0		0.0	
No Name Creek	SW	8	5.8	0.9	2.8	0.4	0.0		0.0		0.0		0.0	
Antelope Creek	NW	8	25.4	0.7	6.4	0.2	0.0		0.0		0.0		0.0	

* No measurements taken

the same time of year, February 12, approximately 285.5 km^2 were without heavy snow cover. This was an increase of 224.5 percent in available winter range in 1974.

Total precipitation in the winter of 1972-1973 was less than in some previous years, 1968 for example (US Department of Commerce 1959-1974). However, persistent cold temperatures from November through April (Table 29) allowed the snow to accumulate. As a result, the May snow pack at the Ryan Park snow transect (2560 m), maintained by the Soil Conservation Service, was the greatest in the 35 years that measurements have been made. Wind velocities were also higher in the winter months of 1972-1973 than in the following year (Table 29).

Use and Charactierstics of the Deer Winter Range

The greatest densities of mule deer in the Beaver Hills occurred on the north end in 1973 and 1974, however, the total area occupied in 1974 decreased considerably from 1973 due to fewer deer. In 1972-1973 only the very steep (50 percent) south, southwest and southeast facing slopes were free of snow from late November through mid-March. These areas ranged from 6.5 km^2 on January 30 to 13 km^2 on March 25. Less steep southerly slopes (30-50 percent) were available for deer use during part of the winter; northerly slopes were available only rarely. During the winter of 1974 the south, southeastern and southwestern slopes below 2438 m were free of snow cover throughout most of the winter. Approximately 10.4 km^2 of open slopes were available on February 12 and approximately 23.3 km^2 on March 25. No elk were observed on Beaver Hills.

Deer densities on the Bennett Peak area were greatest on the juniper covered west and southwest face of the main peak; relatively large numbers also occupied the same exposures on the lower peaks to the immediate east. Although densities were less in 1974, the distribution of deer was about the same. As the snow melted, in mid-April in 1973 and late February in 1974, the deer moved out of

Table 29. Wind velocities and temperatures on mule deer winter range at 8200 feet in the winters of 1972-1973 and 1973-1974.

1972-1973				1973-1974			
Dates	Wind Kmph	Avg. Temp(C°) Max	Min	Dates	Wind Kmph	Avg. Temp(C°) Max	Min
Nov. 9 - Dec. 8	21.1	+2	-8	No records			
Dec. 8 - Jan. 2	22.2	-4	-6	Dec. 1 - Dec. 31	14.3	+0.7	-11
Jan. 2 - Jan. 30	20.6	+2	-12	Jan. 1 - Jan. 31	16.6	-1	-13
Jan. 30 - Feb. 27	16.6	+4	-11	Feb. 1 - Feb. 27	16.6	-1	-11.8
Feb. 27 - Apr. 3	25.6	+3	-8	Mar. 1 - Mar. 31	19.2	+7	-5
Apr. 3 - May 2	25.6	+8	-4	Apr. 1 - Apr. 30	12.9	+8	-3
May 2 - May 16	24.5	+12	+0.2	May 1 - May 16	16.8	+17.4	+2

the rocks and to the surrounding sagebrush flats. One small herd of elk was seen occasionally on the Bennett Peak area.

In 1973 deer at Baggott Rocks were forced to remain in the rocks throughout most of the winter. Deer were unable to move to the sagebrush flats surrounding the Rocks until April due to deep snow. Snow surrounding the Rocks was as deep as 40.6 cm as late as March 14. In 1974 deer used the rocks and the surrounding flats throughout the winter. In addition, deer made extensive use of winter wheat fields and abandoned fields in the area. No elk were observed.

Relative Use of Beaver Hills, Bennett Peak, and Baggott Rocks

The results of pellet transects read on the three areas in 1973 and 1974 are listed in Tables 30 and 31. The Baggott Rocks area received the greatest use, 207.5 deer-days use per hectare, followed by Bennett Peak, 137 deer-days use per hectare, and Beaver Hills, 48 deer-days use per hectare. This use occurred from mid-February to mid-May. The figure for Beaver Hills is in contrast with 87.5 deer-days use per hectare from mid-January to mid-May recorded in 1973.

Data from browse utilization transects for the three areas are presented in Tables 30, 31, and 32. Sagebrush utilization transects for all three areas illustrated extremely heavy past use in the critical areas and heavy use during the winter of 1972-1973 on the Beaver Hills. Sagebrush was less heavily utilized in 1974. Rubber rabbitbrush (Chrysothamnus nauseosus) showed heavy past use with light use in 1974. Antelope bitterbrush was extremely hedged, with average use of annual growth in 1974 exceeding 90 percent. Bitterbrush plants in the Baggott Rocks area underwent such extreme use that their growth form was greatly altered. Only leaders growing along the ground and protected by winter snow showed any semblance of normalcy. The percent of decadent plants found on the critical portion of Bennett Peak was alarmingly high for sagebrush (90 percent), bitterbrush (36 percent) and rubber rabbitbrush (11 percent). In addition, 24 percent of the crowns of mature sagebrush plants measured

Table 30. Sagebrush utilization transects and pellet group counts on the Beaver Hills wintering area in 1973 and 1974[1].

Date		Plant	Form Class by Percent[2] 1	2	3	4	5	6	Age Class by Percent[3] Y	M	D	Percent Dead Crown	Pellet Groups/hectare
1973													
	A	Artemesia tridentata	12	48	32	0	0	8	0	89	11	17.8	1482.6/hectare
	B	A. tridentata	0	0	0	0	4	96	7	79	14	13.4	
	C	A. tridentata	0	0	0	0	0	100					
1974													
	A	A. tridentata	76	8	0	16	0	0	8	88	4	12.9	
		A. tridentata	0	0	0	88	8	4	0	89	11	19.8	1094.7/hectare
		A. tridentata	8	8	0	64	0	20	0	93	7	15.9	

[1] A = Unavailable due to winter snow cover
B = Available during part of the winter
C = Available the entire winter

[2] 1 = No hedging, 0 to 10 percent use
2 = No hedging, 11 to 50 percent use
3 = No hedging, 51 to 100 percent use
4 = Hedging, 0 to 10 percent use
5 = Hedging, 11 to 50 percent use
6 = Hedging, 51 to 100 percent use

[3] Y = Young
M = Mature
D = Decadent

Table 31. Sagebrush utilization transects and pelle group counts on mule deer wintering areas of 1974.

Location		Plant	Form Class by Percent[2]						Age Class by Percent[3]			Percent Dead Crown	Pellett Groups/acre
			1	2	3	4	5	6	Y	M	D		
Bennett Peak													
	A	Artemesia tridentata	12	0	0	24	40	24	10	73	17	15.5	
	B	A. tridentata	20	0	0	28	44	8	18	71	11	6.1	1712.4/hectare
	C	A. tridentata	0	0	0	0	12	88	0	10	90	24.0	
Baggott Rocks													
	A	A. tridentata	0	0	0	32	68	0	0	89	11	11.0	
	C	A. tridentata	0	0	0	0	12	88	0	83	17	17.0	2594.6/hectare

[1] A = Available from early March through spring
B = Available from later February through spring
C = Critical winter range

[2] 1 = No hedging, 0 to 10 percent use
2 = No hedging, 11 to 50 percent use
3 = No hedging, 51 to 100 percent use
4 = Hedging, 0 to 10 percent use
5 = Hedging, 11 to 50 percent use
6 = Hedging, 51 to 100 percent use

[3] Y = Young
M = Mature
D = Decadent

Table 32. Browse utilization transects on mule deer wintering areas of 1974.[1]

Location		Plant[4]	Form Class by Percent[2] 1	2	3	4	5	6	Age Class by %[3] S	Y	M	D	Average Leader Use
Bennett Peak													
	A	Pursha tridentata	0	0	100	0	0	0	0	0	100	0	95.0
	B	Chrysothamnus nauseosus	0	0	100	0	0	0	0	0	100	0	8.0
		C. viscidiflorus	0	64	36	0	0	0	0	0	100	0	6.4
	B	P. tridentata	0	8	88	0	4	0	0	0	96	4	89.0
	C	P. tridentata	0	0	96	0	4	0	0	0	64	36	94.2
		C. nauseosus	0	8	92	0	0	0	0	0	89	11	33.8
Baggott Rocks													
	C	P. tridentata	0	0	100	0	0	0	0	0	95	5	95.0
		C. nauseosus	4	60	36	0	0	0	0	0	100	0	25.4

[1] A = Available from early March through spring
B = Available from late February through spring
C = Critical winter range

[2] 1 = All available, little or no hedging
2 = All available, moderately hedged
3 = All available, severely hedged
4 = Partly available, little or no hedging
5 = Partly available, moderately hedged
6 = Partly available, severely hedged

[3] S = Seedling
Y = Young
M = Mature
D = Decadent

[4] See Appendix I for common names and species authorities.

were dead. All bitterbrush plants measured on the Baggott Rocks area were classed as mature, however, the growth form had been altered so as to make this estimate very subjective and open to some question.

Sedentary deer occupied the above mentioned areas as well as areas extending further south along the North Platte River. The southern most extension of these deer appeared to be Six-mile Gap in North Gate Canyon. Deer wintering in this area occupied steep southerly facing slopes and were forced through deep snow when moving between feeding sites.

In both winters the southern boundary of primary mule deer range was the Skyline, an east to west trending rim dissecting the upper Platte River Valley. Critical winter range on the study area was approximately the same as the distribution of juniper. Elk winter range overlapped with the marginal deer winter areas along the North Platte River.

Deer Distribution in Relation to Snow Depth and Slope

Deer observation on the winter range and attendant snow depths for the winter of 1972-1973 are given in Table 33. Of 1329 observations of deer, 1159 (87.3 percent) were in snow depths less than 46 cm. However, 63 percent of the deer observed in January were in snow depths greater than 46 cm. This situation prevailed because of unusually cold temperatures that allowed snow to accumulate and remain powdery. In mid-January, deer moved out of the deep snow and on to steep south facing slopes with less than 15 cm of snow. The snow conditions of 1972-1973 forced deer to concentrate on a fraction of the approximately 777 km^2 of winter range for an unusually long period of time.

Deer observation on the winter range and attendant snow depths for the winter of 1973-1974 are reported in Table 34. Of 1503 observations of deer, 1496 (99.5 percent) were in snow depths less than 45.7 cm. Those few observations made in snow depths greater than 30.5 cm were made in late January before the deer left the intermediate range and the deep snow was still loose.

Table 33. Deer distribution and attendant snow depths during the winter of 1972-1973.

Year	Month	Snow Depth cm	Number Observed	Percent
1972	Nov.	0	0	0
		2.54 - 15.24	184	53.8
		17.78 - 30.48	158	46.2
		33.02 - 43.18	0	0
		≥ 45.72	0	0
			Total 342	100.0
	Dec.	0	0	0
		2.54 - 15.24	192	100.0
		17.78 - 30.48	0	0
		33.02 - 43.18	0	0
		≥ 45.72	0	0
			Total 192	100.0
1973	Jan.	0	0	0
		2.54 - 15.24	49	18.1
		17.78 - 30.48	19	7.0
		33.02 - 43.18	33	12.2
		≥ 45.72	170	62.7
			Total 271	100.0
	Feb.	0	0	0
		2.54 - 15.24	126	56.2
		17.78 - 30.48	90	40.2
		33.02 - 43.18	8	3.6
		≥ 45.72	0	0
			Total 224	100.0
	Mar.	0	0	0
		2.54 - 15.24	300	100.0
		17.78 - 30.48	0	0
		33.02 - 43.18	0	0
		≥ 45.72	0	0
			Total 300	100.0

Table 34. Deer distribution and attendant snow depths during the winter of 1973-1974.

Year	Month	Snow Depth cm	Number Observed	Percent
1973	Nov.	0	70	62.5
		2.54 - 15.24	38	33.9
		17.78 - 30.48	0	0
		33.02 - 43.18	4	3.6
		≥ 45.72	0	0
		Total	112	100.0
	Dec.	0	36	47.4
		2.54 - 15.24	32	42.1
		17.78 - 30.48	8	10.5
		33.02 - 43.18	0	0
		≥ 45.72	0	0
		Total	76	100.0
1974	Jan.	0	78	23.2
		2.54 - 15.24	51	15.2
		17.78 - 30.48	176	52.4
		33.02 - 43.18	24	7.1
		≥ 45.72	7	2.1
		Total	336	100.0
	Feb.	0	8	2.7
		2.54 - 15.24	159	52.8
		17.78 - 30.48	135	44.5
		33.02 - 43.18	0	0
		≥ 45.72	0	0
		Total	301	100.0
	Mar.	0	642	94.7
		2.54 - 15.24	4	0.6
		17.78 - 30.48	32	4.7
		33.02 - 43.18	0	0
		≥ 45.72	0	0
		Total	578	100.0

Deer observations in relation to aspect and percent slope are contained in Table 35. Of 2781 deer, observations of 2052 (73.8 percent) were on sites with south, west, southeast and southwest exposures. Deer use of northern exposures occurred before early January, while deep snow on these sites was still powdery, or in the spring following snow melt. Deer were seen feeding on bitterbrush in January in powdery snow to depths of 61 cm when nearby sagebrush slopes had little snow cover.

Winter Food Habits and Nutrition

A total of 103 and 87 scat samples were collected in the winter and spring of 1972-1973 and 1973-1974, respectively. Results of the monthly food habits analysis and attendant snow depths at Saratoga, Wyoming are presented in Figure 31. Browse was the most important component of the winter diet followed by grass and finally forbs. Grass and forbs were utilized to the greatest extent in the months of April and May.

Snow depth influenced the amount of browse in the diet as well as the type of browse eaten. Sagebrush was utilized during each month, however sagebrush was utilized less than other shrubs as long as the deer remained on the intermediate range. The sagebrush on this range is a smaller component of the total shrub community. In addition, the dominant sagebrush is mountain big sagebrush which is low in palatibility for mule deer. As depths increased deer moved to the winter range where sagebrush was more abundant and more palatable, due to the presence of Wyoming big sagebrush and black sagebrush. The use of sagebrush continued to increase in late winter and early spring even though snow depths decreased. This probably resulted from the fact that sagebrush retains foliage and nutrient quality throughout the winter (Dietz 1957) while other shrubs, such as bitterbrush, lose much of their foliage and nutrient quality in the course of the winter. When the grasses and some forbs first emerged in late April and early May in 1974, deer began feeding more heavily on

Table 35. Observation of mule deer use of winter range in relation to aspect and percent slope in 1972-1973 and 1973-1974.

Aspect	Number Observed	Percent	Percent Slope	Number Observed	Percent
N	191	6.9	5	39	1.4
S	320	11.5	5-20	1189	42.8
E	68	2.4	21-30	833	29.9
W	657	23.6	31-40	289	10.4
SE	157	5.7	41-50	194	7.0
SW	918	33.0	50	237	8.5
NE	293	10.5			
NW	177	6.4			
Total	2781	100.0		2781	100.0

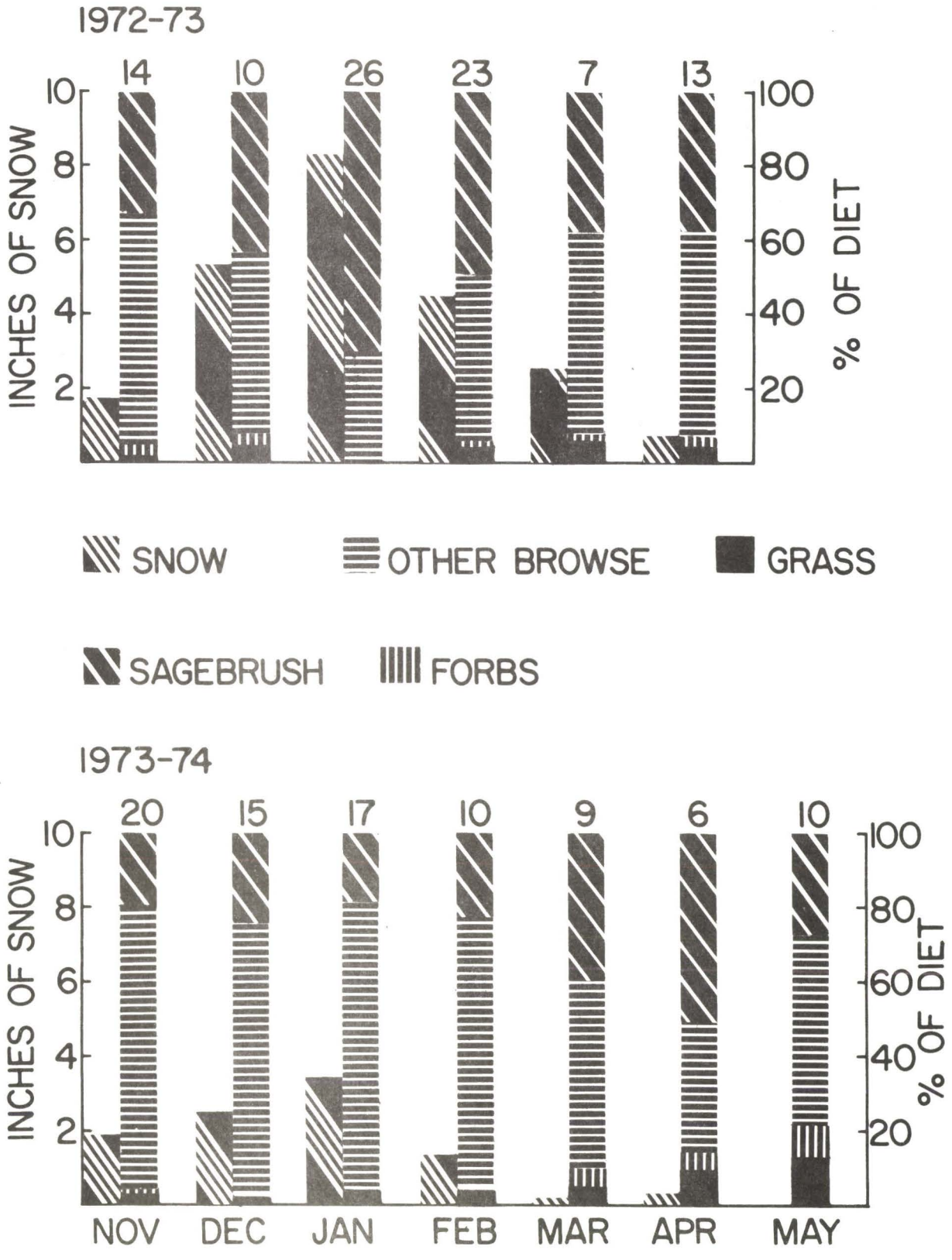

Fig. 31. Winter food habits of mule deer and concomitant average monthly snow depths at Saratoga, Wyoming.

these items. Due to prolonged snow cover and cool temperatures in the spring of 1973 this green-up and the increased use of these plants by deer was delayed. The use of sagebrush decreased in May 1974, apparently as a result of the initiation of new growth in the more palatable species of browse.

Numerous observations of deer feeding in alfalfa haystacks were made in the winter and spring of 1973, yet this apparent heavy use of alfalfa was not reflected in the food items utlized by the deer.

Four deer in various body conditions, all of which had access to supplemental feed (either at feeding sites or haystacks), supplied the rumen juice used in the in vitro DMD studies (Table 36). Digestibility values were higher for the browse species than for alfalfa. Sagebrush (Artemesia tridentata tridentata) had a slightly higher digestibility than the alfalfa. The DMD of bitterbrush, willow (Salix sp.), and rabbitbrush were higher than all other feeds. Values for juniper were slightly greater than those for sagebrush. Differences in DMD between deer were not generally great, although deer 4 digested about 10 percent more juniper and willow than did the other deer. DMD differences between plant species could not be explained on the basis of fiber content or on the physical condition of the deer (Table 36).

Winter Mortality

A large number of animals died during the winter and spring of 1972-1973. Dead animals encountered on the winter range were sexed and placed in age classes and examined for cause of death (Table 37). One hundred fifteen of the 117 animals showed signs of extreme malnutrition. One adult male in fair condition and one adult female in good condition were killed by coyotes. Fawns were present in the mortality sample in approximately the same proportions as they occurred in the 1972 population. In contrast, the proportion of does was much less and the proportion of bucks much higher than in the 1972 population.

Table 36. Fiber components and *in vitro* digestibilities of selected browse species and alfalfa by malnourished mule deer.

	Fiber Components (percent)[a]			DM Digestibility (percent)			
	ADF	Cellulose	Lignin	Deer 1[b]	Deer 2[c]	Deer 3[d]	Deer 4[e]
Bitterbrush	43.8	32.2	10.5	63.8	61.4	62.9	63.6
Willow	42.0	33.1	7.8	58.2	56.6	57.7	66.2
Rabbitbrush	41.3	34.6	5.4	55.8	52.1	56.3	38.9
Juniper	29.3	23.4	5.1	43.4	44.8	46.2	55.4
Sagebrush	34.3	27.7	6.0	44.2	42.2	43.3	47.7
Alfalfa 1[f]	41.5	35.8	4.5	42.3	39.9	43.4	40.9

[a]Components are expressed as the percentage of the total dry matter of the sample.

[b]Adult doe, 61 kg, no kidney fat, trace of heart fat, 39.65 percent fat in femoral marrow.

[c]Adult male, 67 kg, slight kidney and heart fat, 16.55 percent fat in femoral marrow.

[d]Adult doe, 66 kg, omental kidney and heart fat, 88.24 percent fat in femoral marrow.

[e]Adult doe, 42 kg, no visible fat on any organ, femoral fat not measured.

[f]Sample of the alfalfa fed to the mule deer on the feed grounds.

Table 37. Winter mortality sample taken in the spring of 1973.

Sex	Age Class	Number	Percent in Sample	Percent in Population
Male	Fawn	22	18.8	16
	Yearling	18	15.4	4.1
	Mature	14	12.0	9.2
	Old	2	1.7	
Female	Fawn	16	13.7	18
	Yearling	5	4.3	
	Mature	26	22.3	50.5
	Old	11	9.4	
Unknown	Fawn	3	2.5	

Five dead deer were examined on the winter range in 1973-1974. Only one dead deer, a female fawn, died of starvation. Four of the deer were killed by coyotes.

Of the 6 predator-killed deer examined during the 2 years, 3 deer were in fair to good condition, 1 was in poor condition and 1 was extremely malnourished. Four of the 6 were killed in snow 35.6 cm or more in depth.

A population estimate was calculated for summer and fall populations in 1972 and 1973 based on pre- and post-hunt herd ratios (Table 38). Based on these calculations the mule deer herd suffered an 88.9 percent winter mortality in the winter of 1972-1973.

An estimate of productivity was made based on herd classification done in 1972, 1973 and 1974. The productivity value calculated for the deer herd in 1972 was 4.3 percent while the productivity value for 1973 was 16.3 percent. Thus, more adults were added to the population from the fawn crop of 1973 than from the fawn crop of 1972. This increased productivity came even though the proportion of fawns in the herd decreased 242.9 percent from 1972-1973.

The relationship of winter snowfall and temperature to spring pellet group counts the following year made by the Wyoming Game and Fish Department and the U. S. Forest Service was examined by a multiple regression analysis. The relationship between these climatological parameters and the year to year changes in the pellet group counts from 1960 through 1974 was not significant. The greatest variable in the fluctuation of pellet groups per acre was probably the distribution of the deer in relation to the sampling areas.

Initiation of Spring Migrations

The large groups of deer typical of winter range began breaking up in mid-May in 1972 and 1973. Just prior to group dispersal increased agonistic behavior was noted between does. Few deer left the critical winter range in 1973 before this May breakup. In 1974 numerous deer were seen leaving the Baggott Rocks and heading north in early April. Most does moved to fawning areas on the intermediate range at or near

Table 38. Prehunt and post-hunt herd ratios and population estimates based on these ratios for 1972-1973.

Ratio	Pre-hunt		Post-hunt
	1972		
Fawns/100 Does	72		72
Bucks/100 Does	31		26
Total Harvest		427	
Total Population Estimate	17,336		16,909
	1973		
Fawns/100 Does	45		45
Bucks/100 Does	38		30
Total Harvest		109	
Total Population Estimate	2,489		2,380

lower timberline following group dispersal. These deer preferred areas with dense stands of sagebrush interspersed with small groves of aspen.

The final movement to summer range occurred shortly after fawning. Deer began arriving on the summer range in mid-June and all had established summer residence by the first of July. Spring snow melt had little influence on the timing of the migration to summer range. Several deer, probably males, moved to the summer range before fawning had finished. These animals moved up as the vegetation green-up extended up the mountain.

Winter and Spring Movement of Tagged Deer

Eleven deer were marked with neck bands or ear flags in the Baggott Rocks area in February, March and April of 1974. In addition, 4 female deer, 3 adults and 1 fawn, were outfitted with radio transmitters. Efforts at trapping animals were most successful in March following each snow storm.

Winter home ranges of the three adult does that were radio-tagged averaged approximately 259 hectares. Deer 4 spent about 50 percent of her time in the Encampment River bottom and surrounding fields. This deer was tagged in January 1968 as a fawn within 200 m of where she was trapped in 1974. Deer 1 and 5 spent their time in the rocks and surrounding fields but never crossed the Baggott Road and were never located in the river bottom. The radio tagged fawn covered about 86 hectares before she was killed by coyotes, March 31, 1974.

Dispersal of radio tagged deer and other marked deer are illustrated in Figure 29. At the time of dispersal from the Baggott Rocks in the spring deer 4 moved into the river bottom where she remained into the summer. Her only movements were north along the North Platte River. Deer 1 moved to an intermediate range on Platte ridge on or before May 22. She was next located on June 7 at 2743 m on Douglas Creek near Keystone where she fawned. The doe remained at this location through the summer. Deer 5 remained on the intermediate range

from May 24 to June 12. She then abruptly moved to Blackhall Mountain, a distance of 30.6 km. This movement required the deer to change mountain ranges, move across a broad sagebrush flat and cross the North Platte River at flood stage. Two does marked with neck bands were relocated on the summer range, one at Purgatory Gulch and one along the continental divide, both in the Sierra Madre Mountains. Thus, it is clear that deer using this winter range come from both the Sierra Madre and the Medicine Bow Mountains, and this is an important observation when managing this population.

Population Structure

Animal observations grouped according to sex, age class and season are listed in Table 39. The results indicated 31.2 bucks per 100 does on the summer range and 26.3 bucks per 100 does on the winter range in 1972. Yearling bucks comprised 51.7 percent of the males observed on the summer range and 30.8 percent of the males observed on the winter range. The ratio of 72 fawns to 100 does seen in the fall was considered to be the most accurate estimate of fawn production. Herd classification in 1973 yielded 37.9 and 30.3 bucks per 100 does on the summer and winter ranges, respectively. Yearlings comprised 7.5 percent of the males classified on the summer range and 7.4 percent on the winter range. A fawn:doe ratio of 44.9/100 was also observed on the winter range.

Hunter check stations were manned during the 1972 and 1973 mule deer hunting seasons. A total of 35 bucks were checked through the stations in 1972 and 19 in 1973 (Table 40). Two incisors were collected and each animal aged by counting cementum anuli. In addition, four animals collected on the winter range in 1973 for nutrition studies were aged and included in Table 40. Yearlings comprised 28.2 percent of the harvest in 1972 and 15.8 percent of the harvest in 1973. Older animals were represented in approximately the same numbers in both years.

Table 39. Summer and fall deer herd classifications in 1972 and 1973.

Age Class	1972 Summer No.	1972 Summer %	1972 Fall No.	1972 Fall %	1973 Summer No.	1973 Summer %	1973 Fall No.	1973 Fall %
Fawn	93	27.6	71	36.2	42	14.9	40	25.6
Doe	186	55.2	99	50.5	174	61.7	89	57.1
Yearling Male	30	8.9	8	4.1	5	1.8	2	1.3
Adult Male	28	8.3	18	9.2	61	21.6	25	16.0
Total Males	58		26		66		27	
	337	100.0	196	100.0	282	100.0	156	100.0

Table 40. Age composition of mule deer harvested on the Snowy Range in 1972 and 1973.

Years	1972 Number	1972 Percent	1973 Number	1973 Percent
1	11	28.2	3	15.8
2	12	30.7	7	36.8
3	9	23.1	4	21.1
4	3	7.7	2	10.5
5	2	5.1	1	5.3
6	1	2.6	2	10.5
7	1	2.6		
Total	39	100.0	19	100.0

Discussion

Data from numerous studies (Hosley 1956, Loveless 1967, Severinghaus 1947 and Gilbert et al. 1970) indicate that snow depths of over 0.5 m essentially preclude use of range by deer. However, data from this study indicate that depths of .3 m of crusted snow may prevent deer use. If the deer can move out of areas with deep snow, they will migrate to winter range with less snow. Unfortunately, during some winters snow-free areas are so limited that the deer density far exceeds carrying capacity. These areas are below 2600 m, however, so it is unlikely that winter cloud seeding would augment the problem.

Deer migrating from the west side of the Snowy Range as well as the east side of the Sierra Madre range are concentrated on three critical areas in the upper North Platte River Valley each winter. The time spent on these areas depends upon snow conditions. Due to high concentrations of deer on these areas in the past, the vegetation is impoverished. These critical areas are augmented by some marginal wintering areas that are available only in years of average to below average snow cover below 2590 m. However, these areas are important as an intermediate range. The amount of time spent on these intermediate ranges is determined by snow accumulation in November and December.

When deer are forced onto the critical areas early, as they were in 1972-1973, the winter range must be used for a longer time, increased winter mortality results, and deer productivity declines. Not only were there fewer animals surviving in the spring of 1973 but reproduction in 1973 declined markedly. Severe winters in the Missouri River brakes of Montana resulted in decreased fawn production for three years following a severe winter (Richard Mackie, Montana Game and Fish Department, personal communication).

Snow cover does not necessarily play an important role in the timing of spring and fall migrations. Deer seem to prefer certain habitats for the purpose of breeding and fawning.

Because of the effects of snow on winter deer distribution, snow cover also influences the quality of the winter diet. The diet of mule

deer in early winter in 1973-1974 was more varied than in 1972-1973. In 1973-1974 a larger proportion of the diet was made up of more digestible browse species. In both years, during periods of greatest snow cover, sagebrush was the most important food item.

Increased snow pack above 2743 m would not affect mule deer directly. However, snow pack increase below this elevation could magnify already existing problems by reducing still further the available winter range. In addition, downward displacement of wintering elk would increase competition with the deer for the already limited winter resources. Once a winter cloud seeding program is initiated, another consideration is relevant. If severe winters occur on the deer winter range, even though weather modification is not responsible, public sentiment may go against cloud seeding programs because they fail to recognize the critical role the limited size and quality of the winter range play in maintaining the deer population.

No deer mortality was observed that could be attributed to inability to cross flooded rivers or streams.

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THE IMPACT OF SNOW ON HERBACEOUS AND SHRUBBY VEGETATION

D. H. Knight, C. Kyte, B. Rogers, and C. R. Starr

The vegetation is a dominant feature of most terrestrial ecosystems, and as such it influences a variety of other ecosystem characteristics. Thus, if winter precipitation management modifies the vegetation, the ecosystem will change in other ways as well. With this in mind, 5 studies were initiated to evaluate the effect of snow cover duration on the herbaceous and small woody vegetation of the Medicine Bow Mountains above 2700 m. Our research has focused on the question, does snow cover duration have a regulatory effect on plant species composition? If snow cover is an important regulator of species composition, and if winter cloud-seeding has a significant effect on snow cover, then we can expect changes in species composition. Research should then be designed to determine the secondary, indirect changes that might be caused by vegetation modification. The changes may be quite acceptable from a land management perspective, or they may be undesirable.

Additional snow resulting from winter cloud-seeding could modify the plant environment in several ways. First, the growing season may be shortened due to prolonged snow cover. There is some evidence, however, to suggest that a 15 percent increase in snow duration would prolong snow cover by only 3 days (Report to Bureau of Reclamation for the period January 1 to June 30, 1971, Contract No. 14-06-D-5496); the effect of only 3 days would probably be minimal in most cases. On the other hand, we do not know 1) to what extent snow duration limits plant growth; 2) whether or not cloud-seeding would produce only a 15 percent increase; and 3) the extent to which a 15 percent increase might augment the size of snow banks by drifting (perhaps by considerably more than 15 percent). We did not contract to do research on the effect of cloud-seeding on snow duration, but rather the effect

of snow duration on species composition. Our results, and those of others (Billings and Bliss 1959, Johnson and Billings 1962, Weaver 1974), indicate that snow duration can be an important regulator of species composition, possibly as a result of shortening an already short growing season. It has been observed by us and others (Johnson and Billings 1962) that snow duration may vary from year to year by more than 2 weeks in one locality.

If growing season length is not a limiting factor, then prolonged snow cover may enhance plant growth, though possibly still causing changes in species composition. The mechanism could be an interaction between soil moisture and air-soil temperature. By delaying plant growth in the spring, the longer snow duration causes plant growth to occur under conditions of longer days and warmer temperatures, but while soil moisture from the melting snow is still available. It is not known whether this mechanism would be operative.

Of course, additional water is being added to the environment by additional snow. The vegetation adjacent to snow banks may be affected by the additional flow of melt water later into the growing season, assuming the flow is prolonged by cloud-seeding, but the vegetation under the snow bank center would not be affected by the additional water because the soil is probably saturated by even below-normal snow accumulation. Furthermore, Weaver (1974) found that the additional water of deeper snow contributes only slightly to soil moisture availability later in the summer.

There are other mechanisms whereby additional snow might affect the growth and species composition of vegetation, for example, by affecting nutrient availability as a result of changes in decomposition rates or leaching, or by improving the environment for certain pathogens such as snow molds (Bleak and Keller 1973; see also p. 41). There is also the possibility of modifying species composition by reducing year-to-year variation in snow fall and snow cover duration. Some species may depend for their survival on periodic low snowfall years, being able to tolerate only 2 or 3 consecutive heavy snowfall years. The significance of these potential mechanisms is not now known.

In sum, since the direct effect of adding snow on top of snow is probably minimal, we believe the principal mechanism by which cloud-seeding could modify the vegetation is somehow related to an increase in snow duration. As indicated earlier, there is still some question about whether cloud-seeding will prolong snow cover for more than a few days. In part, our research was designed to determine whether those few days of additional snow cover would be ecologically significant to plant species composition.

Five separate studies were initiated to evaluate the effect of snow duration on species composition, plant growth, and plant phenology. The studies are presented in the following sequence: 1) Subalpine meadow vegetation in relation to environment at Headquarters Park, 2) The response of meadow species composition to artificially prolonged snow cover, 3) Understory species composition in relation to snow duration in subalpine forests, 4) The abundance and growth of Vaccinium scoparium in relation to snow duration, and 5) Plant phenology in relation to snow duration. The second study is described, but results will not be available for at least another 2 years.

I. Subalpine Meadow Vegetation in Relation to Environment at Headquarters Park.[1]

Headquarters Park is a complex of subalpine meadows surrounded by subalpine fir-Engelmann spruce forest on the western slopes of the Medicine Bow Mountains. The Park lies in the North French Creek and South Brush Creek drainages, and varies in elevation from 3048 m to 3219 m. It covers an area of about 1.3 km^2. Mean annual precipitation is approximately 119 cm, most of which comes as snowfall

[1] A more detailed presentation of this study is available in Starr, C. R. 1974. Subalpine meadow vegetation in relation to environment at Headquarters Park, Medicine Bow Mountains, Wyoming. M.S. Thesis, Dept. of Botany, University of Wyoming.

(U. S. Weather Bureau, personal communication). Most of the area is underlain by undivided glacial deposits including drift, outwash deposits, loess and varved shale. An exception is the area just below Silver Lake, which is underlain by Medicine Bow Peak Quartzite (Houston, et al. 1968).

Fifty stands were selected, each 5 x 10 m in size. Stands were selected for homogeneity of vegetation, lack of recent heavy grazing pressure, and so that the full range of meadow types in the area would be included. We decided to use small stands so that correlations between environment and species composition might be more obvious.

Cover and frequency data were obtained in each stand using 20 x 50 cm rectangular quadrats and the Daubenmire (1959) canopy coverage method (20 quadrats per stand). Location of quadrats within each stand was done systematically. Floristic data for each stand were taken twice during the summer, once in mid to late July, and again in mid-August. The maximum of the two values was used for each species. Examination of the stands prior to sampling showed that no early growing species were missed.

The following environmental measurements were made in each stand: snow release date, soil temperature, soil moisture and soil texture. The snow release date was considered to be the date on which approximately 90% of the stand was estimated to be snowfree.

Soil temperature was measured at 2 depths (-5 and -20 cm) using copper-constantan thermocouples and a null-detector microvoltmeter. Thermocouples for each depth were placed at two locations within each stand. Readings in all stands were taken five times during the summer between the hours of 12 and 2 PM on two consecutive days of similar weather. The dates were July 11-12, July 17-18, July 26-27, August 8-9 and August 25-26. A two day period was required since not all 50 stands could be sampled between 12 and 2 PM on one day. The readings for the two locations at each depth in each stand were averaged.

Soil moisture was determined gravimetrically (Gardner 1965). Composite samples were taken from three locations within each stand at depths of 4-6 cm and 19-21 cm. The three locations were selected

randomly with the restriction that none were within 0.5 m of thermocouples or vegetation quadrats. Samples were taken five times during the summer, at the same time as the temperature determinations. The total composite soil samples for each depth and stand were used for texture analysis, using the Bouyoucos (1927) method.

Direct and indirect gradient analysis techniques were used to examine the relationships between species composition and environment (see Starr (1974) for details).

Results[1]

The results indicate that, of the environmental factors studied, only minimum soil moisture during the summer is highly correlated with the species composition of subalpine meadow vegetation in Headquarters Park. Soil temperature had a slight tendency to be inversely related to soil moisture. This was expected as moist soils heat up less rapidly than drier soils.

Snow release date was not correlated with species composition in our ordination. All stands became snow-free within fourteen days of each other, and most within nine days; the latest observed release date was July 5. Neither geologic substrate nor soil textural properties were correlated with species distribution, except in the stands with peat soils which were also the stands that remained saturated during most of the growing season.

Discussion

On the basis of these results, it seems unlikely that increased snowfall from cloud-seeding would modify the plant species composition of the Headquarters Park meadows, unless 1) snow duration is prolonged beyond July 5; 2) the additional snowfall is sufficient to raise the minimum soil moisture reached during the growing season, which is

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[1] Graphs and tables for this particular study are not presented due to their bulk; consult Starr (1974).

unlikely (Weaver 1974); 3) the additional snow fall is sufficient to modify the soil moisture regimes illustrated in Fig. 10; 4) new snow banks are formed; or 5) some now unknown, indirect effects lead to vegetation modification, for example, by providing a more favorable habitat for pocket gophers. Frank (1973) studied a Colorado mountain grassland, and concluded that a 10 percent increase in peak snowpack would increase snow duration by only 1.5 days and would have little, if any, effect on productivity or use. He did not study species composition, and all the snow was gone from his study area by early June.

Of course, our results apply only to the Headquarters Park area. Had we studied the meadows over a larger area, and included some study areas that are snow-free before June 20 and others that are snow-covered until mid-July, we might have observed an effect of snow duration on species composition. Billings and Bliss (1959), working nearby, but at a higher elevation, found that snow banks persisting into mid-July had a considerable effect on species composition. Their results suggest that snow duration becomes a significant limiting factor only if snow persists until after about the first week of July. Weaver (1974), however, found that snow persisting only into mid-June had an effect on meadow species composition on the Bangtail Mesa in Montana (2070 to 2440 m elevation). Most sites in the Medicine Bow Mountains above 2700 m are still snow-covered in mid-June. The apparent discrepancy between our data and Weaver's data could be due to 1) a difference in duration of the growing season into the summer, or 2) a longer growing season requirement by the species that Weaver studied.

Weaver (1974) found that plant species diversity, vegetation cover, and primary productivity of Festuca idahoensis meadows[1] in Montana

[1] Festuca idahoensis meadows were not observed in Headquarters Park, but they do occur elsewhere in the Medicine Bow Mountains.

become progressively lower the longer snow persists into late May and early June. He lists species that become more abundant or less abundant with longer snow duration, as do Gjaerevoll (1956) and Dahl (1956).[1] Lists of increasers and decreasers did not emerge from our study in Headquarters Park, perhaps because there are other environmental factors that mask or preclude the effect of snow duration until July 5, but such lists were derived for the forest understory adjacent to the meadows (see page 185).

In view of the fact that Billings and Bliss (1959), Johnson and Billings (1962, Fig. 32), and Weaver (1974) observed a significant effect of snow duration on species composition in alpine and subalpine herbaceous vegetation in the Rocky Mountains, it may seem odd that we did not. The following points are relevant:

1. A period of only 14 days (most often 9 days) separated the first snow-free stand from the last, and in no stand did snow persist beyond July 5 in 1973. Weaver (1974) conducted his study in an area of different species composition and different environment, where snow duration varied from May 22 to June 15 (24 days); and Billings and Bliss (1959) and Johnson and Billings (1962) studied alpine vegetation where cover persisted until at least mid-July.
2. Unlike the other studies, we examined a wider range of meadow vegetation, in order to determine what environmental factors were most correlated with species composition. Minimum soil moisture during the growing season was so dominant in its effect that the other environmental factors we measured, such as snow duration, were not obviously correlated with species composition. By studying only the dry meadows or mesic meadows separately and in greater detail, we might have been

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[1] Some species listed by Weaver (1974) are also found in the meadows of Headquarters Park. Their response to snow cover duration in Montana could be quite different than in southern Wyoming, and therefore they are not listed in this report.

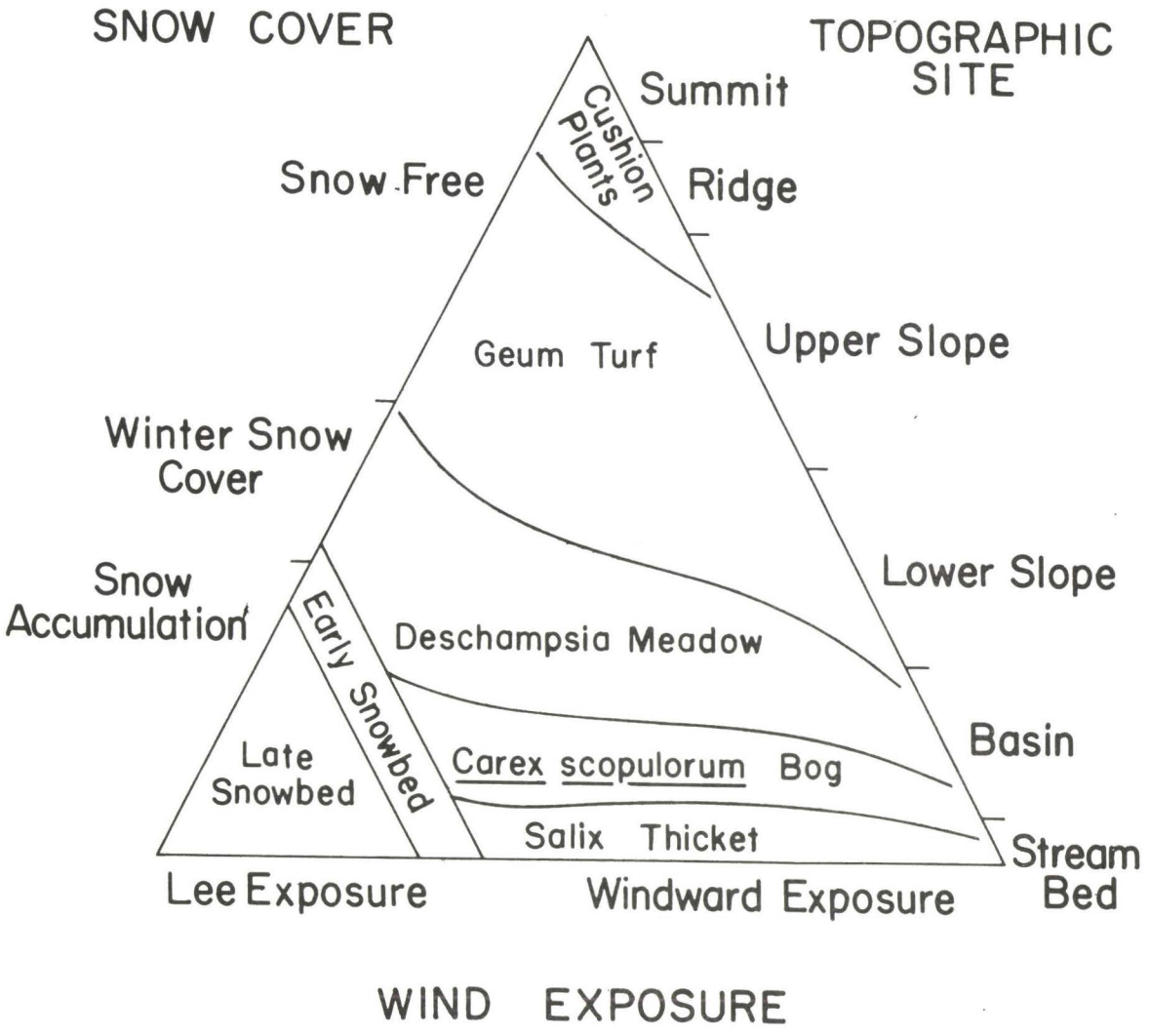

Fig. 32. Mosaic chart of major vegetation types on the Beartooth Plateau. Note that snow cover is a principle factor (after Johnson and Billings 1962) regulating species composition.

able to demonstrate an effect of snow duration on species composition. The existing information suggests, however, that the effect would be small as long as snow cover does not persist beyond July 5. Apparently most, if not all, of the plant species in the meadows have evolved adaptations to tolerate snow cover that persists into early July. It is possible that snow cover persistence in any one stand varies considerably from year to year due to different amounts of snowfall, different timing of snowfall, and different rates of snowmelt due to varying climatic conditions in the spring. The effect of this year-to-year variability would be to make most or all of the species tolerant to snow cover that persists until early July, according to our data. It would be desirable to have a long-term record of year-to-year variability of snow duration on specific sites, and to know the significance of this year-to-year variability for the survival of some species.

II. The Response of Meadow Species Composition to Artificially Prolonged Snow Cover.

An experiment was initiated in the spring of 1973 to see if meadow species composition could be changed by artificially prolonging the duration of snow cover by 8-10 days. A dry meadow at 3109 m and a mesic meadow at 3054 m were utilized for this experiment, both located in Headquarters Park[1]. A randomized complete block design was used, with 5 pairs of plots in each meadow. The plots were each about 1.5 m^2 in size, and the pairs were selected so as to be as similar as possible. One of each pair was randomly selected to receive a snow treatment, which consisted of shovelling by hand a sufficient amount of snow onto the

[1] The dry meadow and mesic meadow correspond to Headquarters Park I and Headquarters Park II, respectively, referred to on p. 24 and page 25.

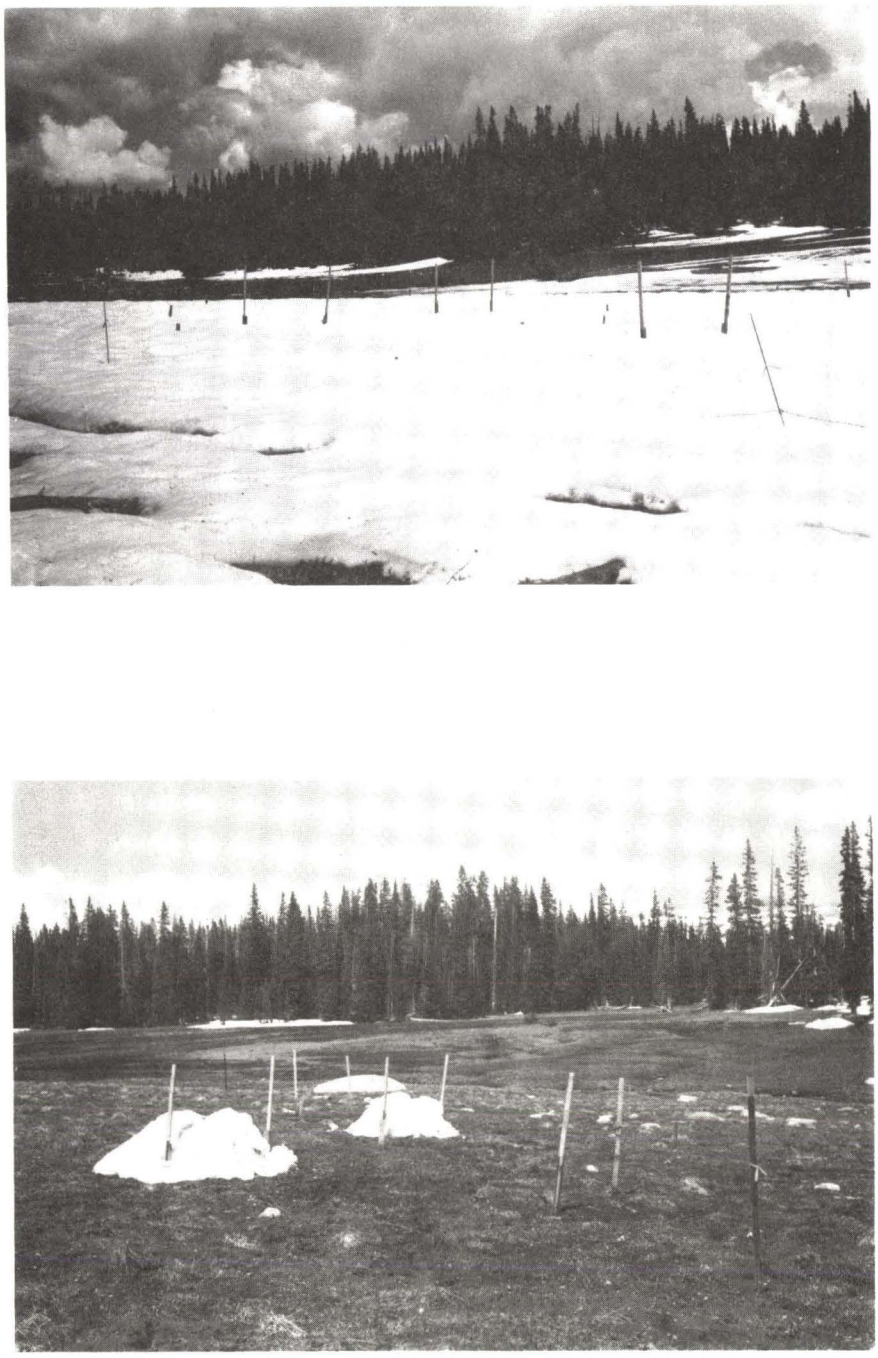

Fig. 33. Two photos of the Headquarter Park II study area, a mesic meadow, where snow is being artificially prolonged on small plots. The top photo was taken on June 27, 1973 (snow depth ca. 25 cm) and the bottom photo on July 1, 1973, just before enlarging the snowbanks by shovel with snow from the adjacent forest behind the photographer.

plot so that the plot remained snow covered for 8-10 days longer than the control plot, Fig. 33.

The treatment has now been applied twice, once in the spring of 1973 and again in 1974. No data have yet been taken on the plots. We plan to apply the snow treatment for 2 more years and to determine by analysis of variance if there is any treatment effect on species composition. No effect is visually apparent after two years, but changes brought about by prolonged snow cover may not occur until the plant's stored energy reserves have been depleted and this may require several years. A full report on this experiment will be submitted in 1977.

III. Understory Species Composition in Relation to Snow Duration in Subalpine Forests.

For several years we have observed the patchy distribution pattern of understory species in the subalpine forests above 2700 m in the Medicine Bow Mountains. The possibility exists that late-persisting forest snowbanks might be a cause of this patchy distribution, and in early July, 1972, the peripheries of over 20 snow banks were staked, Fig. 34. It was striking to observe, after the snow had disappeared, how the stakes exactly delimited vegetation patches in several localities. These preliminary results encouraged us to study forest understory species composition along snow duration gradients.

Eighteen snow duration gradients were studied at two locations in the high elevation forests on the west side of the Medicine Bow Mountains near Headquarters Park, Fig. 35. One forest at 2900 m was dominated by lodgepole pine, the other at 3090 m by Engelmann spruce and subalpine fir. At each location snowbanks were selected in mid-June while snow cover was continuous. Transects 1 m wide and approximately 10 m long were marked on what appeared to be potential snowbanks at that time. At four or five day intervals during the time of snowmelt, the snow-free portions of each transect were marked so that it would later be known when that portion of the transect

Fig. 34. Photos taken in late June and early July (bottom) of two forest snowbanks. The dashed line on the lower photograph defines a zone near the snowbank where Vaccinium scoparium is infrequent, probably because of the shortened growing season caused by the snowbank.

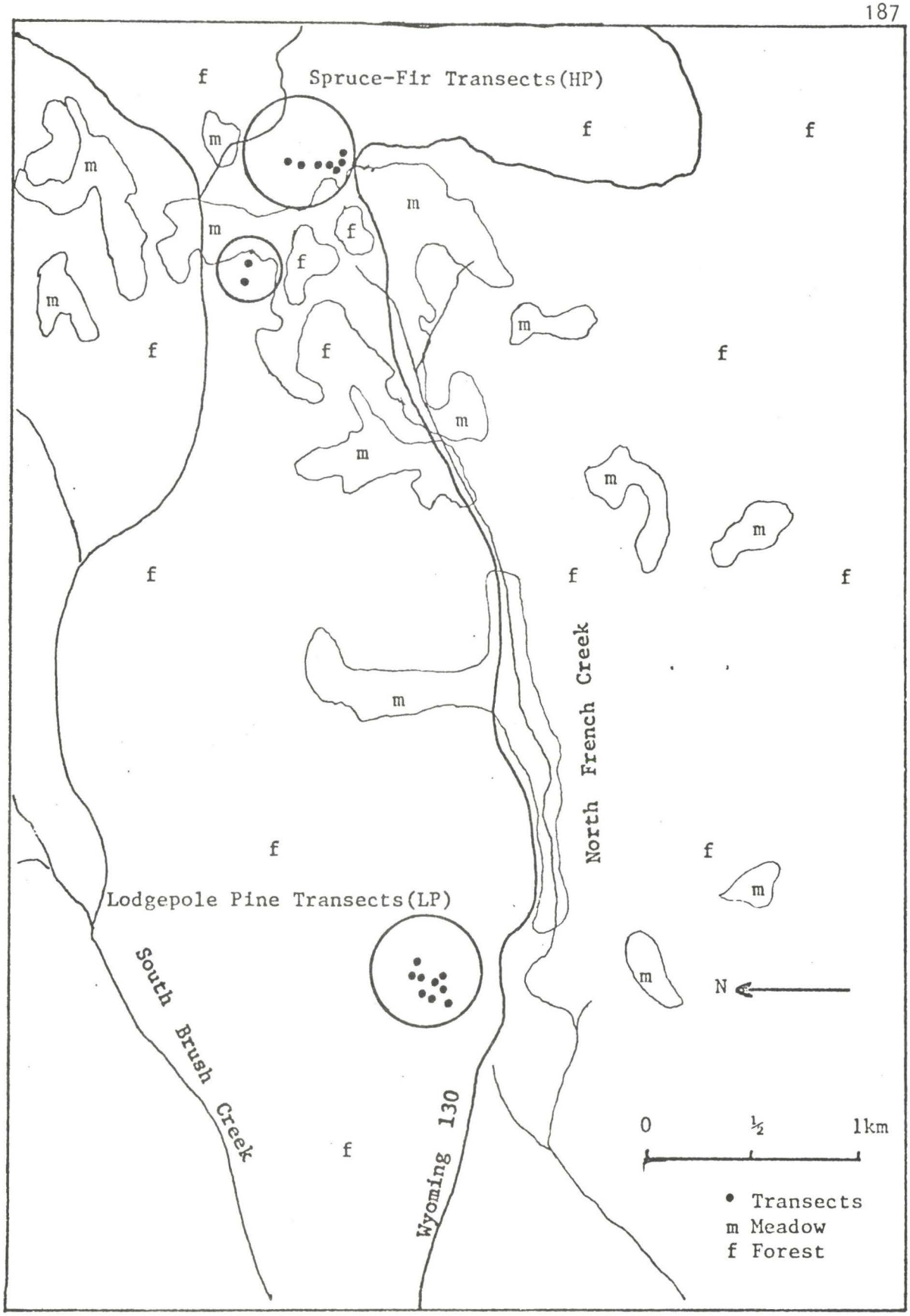

Fig. 35. Location of the forest snowbank transects on the west slope. Each dot within the 3 circles is one transect.

became snow-free. Approximately 15 days after snow was gone from the entire transect the species were sufficiently well developed to be identified (July 15 for the lodgepole pine forest, July 28 for the spruce-fir forest). At this time species cover in each phenological segment of all the transects was estimated using two rows of contiguous 20 x 50 cm quadrats and the canopy coverage method (Daubenmire 1959).

Results

Tables 41 and 42 show that several species have trends in percent cover along the snow duration gradient. In the lodgepole pine forest, which was clear of snow by June 29, Carex geyeri, Carex rossii, and possibly Arnica cordifolia decrease in cover with late-persisting snow; all of these species are rare in the spruce-fir forest where the earliest snow release was around June 30 ($\pm$2 days). Hieracium gracile and possibly Erigeron peregrinus increased in cover with longer snow duration in the pine forest; the dominant shrub, Vaccinium scoparium, had no significant change, contrary to the results in the spruce-fir forest.

In the spruce-fir forest, where snow persisted until mid-July, Vaccinium scoparium had a very pronounced decline, and was the only species to do so without question. The data are adequate to suggest that 14 species either increased with longer snow duration or at least are able to tolerate late-persisting snow (Androsace sp., Arnica latifolia, Calamagrostis purpurascens, Erigeron peregrinus, Erythronium grandiflorum, Hieracium gracile, Poa cusickii, P. nervosa, P. reflexa, Polytrichum juniperinum (and other mosses), Ranunculus alismaefolius, R. eschscholtzii, Sibbaldia procumbens, and Thlaspi alpestre). It is possible that these species are able to persist because of the reduced competition from the otherwise dominant Vaccinium scoparium (and possibly Carex spp.), not because they require long periods of snow cover or because they are better adapted to a growing season that begins later. In another study conducted nearby, we observed that the following species were negatively associated with Vaccinium scoparium: Antennaria sp., Arnica cordifolia, Carex sp.,

Claytonia lanceolata, Lewisia pygmaea, Senecio sp., and Sibbaldia procumbens . If winter snowpack augmentation leads to a reduction in the abundance of Vaccinium, then these other species could increase in abundance.

Discussion

The forest data show quite clearly that snow duration is a regulator of understory species composition. Several questions are now raised.

First, what is the mechanism that causes the changes in species composition? The answer to this is not known, though it is related in some way to snow duration and probably requires several years of snowbank formation in one area to be effective. Our staked snowbank observations during the last 3 years indicate that forest snowbanks are formed in approximately the same area each year. Their position is probably determined primarily by the structure of the forest canopy; timber harvest is known to affect snow accumulation patterns.

A second question relates to the actual land surface area affected by long-lasting snowbanks. In an attempt to determine natural snow cover in early July, we conducted a survey over approximately 5 km^2 near Headquarters Park, using about 10 km of transects in the forest. On July 12 approximately 8 percent of the area was still covered by snowbanks. Even if cloud-seeding increases this area to 12 percent, the effect on the forest understory vegetation in the area is likely to be small. Banks would, perhaps, be increased in size somewhat, and the size of the Vaccinium-free patches would be increased correspondingly, since Vaccinium does not tolerate very well snow cover beyond the 1st week in July (Table 42). We have not yet observed any undesirable attributes about those vegetation patches where Vaccinium cannot survive. However, it is a dominant species in the understory of most of the forests in the Medicine Bow Mountains, and to reduce its cover by, say 40%, could be undesirable. Based on what we now know, it seems unlikely that winter snowpack augmentation would increase snow cover by more than a few percent above what would have

occurred anyway, and, if anything, changes in species composition would occur over no more than perhaps 5 to 10 percent of the area. The area affected would be located around the periphery of any enlarged snow banks that exist in early July, or under new snow banks that are created by cloud-seeding activity. We do not now know of rare or endangered species that would be driven to extinction by augmented snowfall, though they may exist.

As indicated previously, it is very important in evaluating ecological impact to know by how much snowfall will be augmented, how that additional snow will normally be distributed, and about how many days snow cover duration will be prolonged by cloud-seeding. We have been led to believe by the literature and personal communication that snowfall may be augmented by about 15 percent during light to medium snowfall years, that cloud-seeding will not be done during naturally heavy snowfall years, that no new snow distribution patterns will arise because of cloud-seeding, and that snow duration might be increased by 2 or 3 days as a result of a 15 percent snowpack increase (Leaf 1971, Frank 1973). Our conclusions about a minimal effect on the vegetation assume that the above information is correct. Will cloud-seeding increase snowfall by only 15 percent in the Medicine Bow Mountains? Will a 15 percent increase in snowpack shorten the growing season by only 2 or 3 days in the forest understory as well as in open meadows? Will new snowbanks be formed? Will cloud-seeding reduce year-to-year variability in snow duration and thereby reduce the abundance of species that require this variability? These are examples of the kind of questions that should be answered with confidence[1].

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[1] The potential effect of silver toxicity to plants is considered beginning on page 329.

TABLE 41. The percent cover of all species encountered in 9 transects along a snow duration gradient in a lodgepole pine forest at 2900 m elevation. Carex geyeri is the only species with a significant trend, judged using the Kolmogorov-Smirnov two-sample non-parametric test ($0.01<p<0.05$). See Appendix I for species authorities and common names.

Species[1]	Approximate Date of Snow Release in 1973																																
	June 17[2] Transect Number										June 22 Transect Number										June 27 Transect Number												
	1	2	3	4	5	6	7	8	9	$\bar{x}$	1	2	3	4	5	6	7	8	9	$\bar{x}$	1	2	3	4	5	6	7	8	9	$\bar{x}$			
Abies lasiocarpa	-	-	-	-	.1	.3	-	-	.1	+	-	-	-	-	-	1.1	-	-	.1	+	-	-	-	-	-	-	-	-	-	-			
Arnica cordifolia	-	-	.8	.4	.4	-	-	-	1.1	.3	-	-	.1	-	-	1.4	-	.3	1.4	.4	-	-	-	-	.1	.3	.3	-	-	+			
Arnica latifolia	-	.4	-	-	-	-	-	-	-	+	-	.5	-	-	-	-	-	-	-	+	-	.8	-	-	-	-	-	-	-	+			
Carex geyeri	6.0	6.6	3.8	.5	18.5	14.9	22.6	2.9	-	8.4	3.3	5.0	1.4	.9	6.9	5.7	11.6	2.6	1.5	4.3	.5	3.2	.1	.2	3.5	.7	3.3	-	-	1.3			
Carex rossi	.3	4.3	.5	1.6	-	.3	-	-	.8	.9	-	-	1.7	.5	.1	1.1	-	1.5	-	.5	.2	-	.1	.9	-	-	-	.3	.7	.2			
Erigeron peregrinus	-	-	-	.9	-	-	-	-	-	+	-	-	-	1.3	-	-	-	-	-	+	-	-	-	24.5	-	-	-	-	-	2.7			
Erigeron sp.	-	-	-	-	-	-	2.8	-	-	+	-	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	0			
Hieracium gracile	-	1.4	1.1	-	2.0	4.5	-	3.3	-	1.4	-	.3	3.9	-	7.1	-	3.0	7.6	-	2.4	-	-	10.8	-	1.9	4.9	.3	11.1	6.1	3.9			
Lupinus argenteus	-	.3	.1	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	0	-	-	.8	-	-	-	-	-	-	+			
Vaccinium scoparium	53.4	62.4	68.9	78.1	56.2	31.1	63.1	56.3	79.2	61.0	64.7	56.0	53.1	75.4	56.0	60.2	81.3	45.5	77.9	63.4	66.8	61.3	65.5	56.4	53.2	62.2	71.4	25.6	64.4	58.5			
Mosses	3.4	.6	.4	.6	-	-	-	-	-	.6	4.5	2.3	.7	.8	.4	-	-	7.4	-	1.8	9.5	.6	.3	4.1	1.1	-	.1	.7	-	1.8			
Number of quadrats used for the sample	20	20	20	20	14	19	18	20	19		16	10	44	14	18	14	14	29	24		14	21	10	58	29	55	73	38	40				

[1] Nomenclature follows Harrington (1954)

[2] The dates given should be read as $\pm$ 2 days.

TABLE 42. The percent cover of all species encountered in 9 transects along a snow duration gradient in a spruce-fir forest at 3040 m elevation. Vaccinium scoparium and Polytrichum juniperinum have significant trends, judged using the Kolmogorov-Smirnov two-sample non-parametric test ($0.01 < p < 0.05$). See Appendix I for species authorities and common names.

Approximate Date of Snow Release in 1973

Species[1]	June 30[2] Transect Number						July 4 Transect Number										July 9 Transect Number										July 14 Transect Number									
	1	2	3	4	9	$\bar{x}$	1	2	3	4	5	6	7	8	9	$\bar{x}$	1	2	3	4	5	6	7	8	9	$\bar{x}$	3	4	5	6	7	8	9	$\bar{x}$
Androsace sp.	.5	-	-	-	-	+	1.8	-	-	-	.1	-	-	-	-	+	.3	-	-	-	-	-	1.3	-	-	+	-	-	-	-	-	-	-	0
Arnica latifolia	-	-	-	-	-	0	-	-	-	-	20.8	.1	2.2	-	-	2.6	-	-	-	-	5.2	1.9	2.1	3.8	-	1.4	-	-	2.3	.5	1.1	8.0	-	1.7
Calamagrostis purpuracens	-	-	-	-	-	0	-	-	-	-	-	-	-	9.3	-	1.0	-	-	-	-	-	-	-	14.3	-	1.6	-	-	-	-	-	4.4	-	.6
Carex geyeri	2.1	-	-	-	-	+	-	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	0
Carex rossi	-	-	.8	.2	-	+	-	-	1.9	-	-	-	.8	-	-	+	-	-	-	.1	-	-	-	-	-	+	-	-	-	-	-	-	-	0
Epilobium hornemanni	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	.5	+	-	-	-	-	-	-	1.5	+
Erigeron peregrinus	-	.1	.1	-	21.5	4.3	-	-	-	-	.9	-	1.8	32.5	16.3	5.7	-	-	1.0	-	2.8	-	-	14.6	8.5	3.0	4.0	-	-	-	-	4.5	-	1.2
Erigeron sp.	6.3	-	-	-	.5	1.4	2.7	-	-	-	.8	-	.1	1.6	20.8	2.9	-	-	-	-	1.8	-	.2	2.9	.2	.6	-	-	.8	-	-	-	-	+
Erythronium grandiflorum	-	-	-	-	-	0	-	-	-	-	-	-	.3	.8	-	+	-	-	-	-	.1	-	.2	-	-	+	-	-	.1	-	.5	1.6	-	+
Hieracium gracile	7.6	9.5	.1	-	-	3.4	11.0	1.6	1.3	1.0	13.6	4.0	11.6	8.0	29.5	9.1	1.9	-	6.4	2.9	4.4	5.0	17.1	5.1	31.0	8.2	11.8	-	9.0	4.8	10.6	1.9	41.5	11.4
Ligusticum porteri	-	.1	-	-	-	+	-	.1	-	-	-	-	-	1.5	-	+	-	-	-	-	-	-	-	-	-	0	-	-	-	-	-	1.5	-	+
Luzula spicata	-	-	-	-	-	0	-	-	-	-	-	-	-	.1	-	+	-	-	-	-	-	-	-	.3	-	+	-	-	-	-	-	.1	-	+
Poa cusickii	-	-	-	-	-	0	-	-	-	-	-	-	.4	-	-	+	-	-	-	-	-	-	.7	-	-	+	-	-	2.3	-	.6	-	-	+
Poa nervosa	3.4	-	-	-	-	.7	3.5	-	-	-	1.8	-	1.2	-	-	.7	2.9	-	4.4	-	1.7	-	6.1	1.3	-	1.8	-	-	-	-	7.1	1.5	-	1.2
Poa reflexa	1.3	2.3	-	.2	-	.8	3.1	1.6	-	1.0	.3	3.8	-	-	-	1.1	9.4	-	-	1.2	4.9	.3	-	-	-	1.8	-	4.1	3.9	-	-	-	-	1.1
Polygonum bistortoides	-	2.1	-	-	-	+	-	-	-	-	-	-	-	-	.1	+	-	-	-	-	-	-	-	-	-	0	.1	-	-	-	-	-	-	+
Ranunculus alismaefolius	-	-	-	-	-	0	-	-	-	-	-	-	-	.1	-	+	-	-	-	-	-	-	-	23.8	-	2.6	-	-	-	-	-	12.3	-	1.8
Ranunculus eschscholtzii	-	-	-	-	-	0	.4	-	-	-	.8	-	-	3.0	-	.5	-	-	.1	-	2.1	-	1.4	25.9	7.3	4.1	3.3	-	8.6	-	1.1	12.5	-	3.6
Sibbaldia procumbens	1.8	-	-	-	-	+	1.0	-	-	-	-	-	-	1.0	2.5	.5	-	-	.1	-	3.3	-	-	3.5	1.0	.9	-	-	1.5	-	-	.3	1.0	.4
Thlaspi alpestri	.6	2.5	-	-	-	+	.7	-	-	-	-	-	-	-	-	+	.5	-	-	.2	-	-	-	-	-	+	-	-	2.5	-	-	-	-	+
Vaccinium scoparium	53.1	84.1	75.4	71.4	98.5	76.5	37.8	66.9	58.1	62.7	52.5	54.9	69.2	62.9	43.0	56.4	37.6	73.6	42.4	65.8	29.8	39.8	12.7	9.3	1.0	34.5	5.8	27.5	24.6	18.1	2.0	.4	-	11.2
Polytricum juniperinum	.8	-	-	1.9	-	.5	8.1	-	1.1	2.5	5.6	1.0	-	6.9	-	2.8	11.0	-	8.6	13.2	4.7	-	-	28.1	28.0	10.4	22.6	19.3	34.1	-	-	27.5	75.0	25.5
Other mosses	-	-	-	-	-	0	-	-	.1	.1	-	.3	.1	-	5.0	.6	-	-	2.0	1.8	1.2	-	2.7	-	11.5	2.1	5.4	-	4.3	1.1	1.1	-	46.1	8.3
Number of quadrats used for the sample	20	20	20	33	10		40	20	28	34	20	20	20	20	10		20	20	20	45	30	20	14	20	10		20	20	40	20	20	20	10	

[1] Nomenclature follows Harrington (1954)

[2] The dates given should be read as ± 2 days.

IV. The Abundance and Growth of *Vaccinium scoparium* Leib. in Relation to Snow Duration.

Vaccinium scoparium Leib., commonly called huckleberry or grouse whortleberry, is a small shrub that appears to be by far the most common plant in the understory of most lodgepole pine forests and spruce-fir forests in the Medicine Bow Mountains. Where huckleberry occurs, it often forms a carpet of green on the forest floor. Because of this, and because we know it is sensitive to snow duration, we initiated a study to learn as much as possible in the time available about the ecological characteristics of *V. scoparium*. Only with this information can we confidently predict 1) the effect of snow duration on the forest understory, and 2) the ecological significance of this effect to the forest as a whole. Studies were conducted in the field and laboratory between May of 1972 and September of 1974.

The principal study area was located at 3,091 m in a mature spruce-fir stand adjacent to Headquarters Park on the west slope of the Mountains. Oosting and Reed (1952) located two of their stands in this area and they present a detailed description of the vegetation of these virgin forests. This stand was selected for study because of its undisturbed nature, the presence of numerous late-lying snowbanks within the forest, the well-developed understory dominated by *V. scoparium*, and its accessibility. Pieces of charcoal found in the top 15 cm of soil indicate a history of burning. Pleistocene glacial deposits form the substrate. Fig. 36 is a map of the study area. Trees over 10 cm dbh and the borders of snowbanks, as they existed on July 6, 1973, are shown on the map.

V. scoparium is a small (usually $\leq$ 4 dm in height) green-stemmed ericaceous shrub which grows in clones. Reproduction is almost exclusively vegetative by rhizomes. No seedlings were observed in this study. Small, bell-shaped, whitish, insect-pollinated flowers are produced as the leaves are expanding soon after the plants are released from snow. The small deciduous leaves are born on slender, chlorophyllous, grooved twigs. In the Medicine Bows it is found from about 2,424 m to

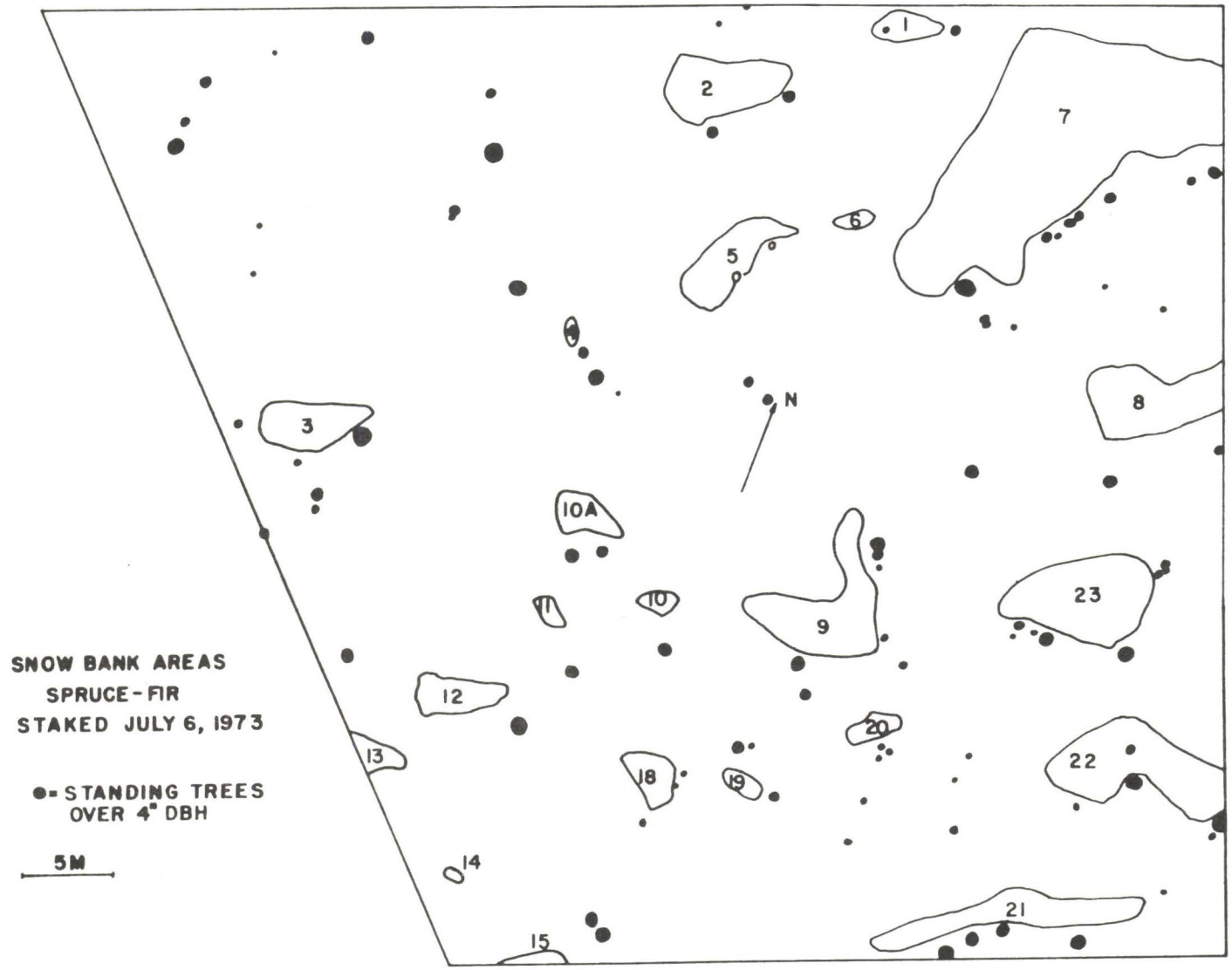

Fig. 36. Map of snowbanks in the Headquarters Park spruce-fir forest study area on July 6, 1973. Solid dots are trees of corresponding size.

about 3,333 m. The habitat is primarily in the forest understory, although it is found in the open at higher elevations (above about 3,182 m). Janke (1968) observed a similar distribution of V. myrtillus in the Colorado Front Range and suggested that reduced competition allowed the plant to grow in the open at higher elevations. The plant can be found growing in subalpine meadows along fallen logs and around the margins of small trees and rocks at lower elevations. Its survival in these microsites may be due to higher available soil moisture. The plant survives in similar situations following a clear-cut or forest fire.

Although V. scoparium may be found growing at 2,424 m, it is only an occasional component of the forest understory at that elevation, occurring generally on north-facing slopes in cooler, more moist sites. Above about 2,727 m it becomes the dominant species in the forest understory and remains dominant to timberline. At higher elevations V. scoparium can be found on the leeward side of krummholz islands and boulders. In some high elevation forests there appear to be rings of more vigorous Vaccinium growth around the boles of trees. These are the first areas to become snowfree in the spring and growth was observed to be initiated in these plants first. V. scoparium is absent from very wet or marshy areas.

Nearly all the roots and rhizomes of the clones examined are contained in the F-layer. Oosting and Reed (1952) stated, "Practically all of the roots of the lesser vegetation, especially those of V. scoparium, were in the F-layer and the very uppermost part of the A horizon." Janke (1968) found that V. myrtillus is poorly adapted to conserving water. If V. scoparium is also poorly adapted to conserving water, then the presence of most roots in the F-layer could be an adaptation to utilize water intercepted by the litter during the growing season.

Although V. scoparium is a very common shrub, it is apparently only rarely utilized by foraging deer, elk, and other mammals. Even insects seem to avoid eating the foliage. The only consumer of any import that we observed was a rust of the genus Pucciniastrum.[1]

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[1] One species we have observed is P. goeppertianum (Kuehn) Kleb.

Janke (1968) made similar observations for V. myrtillus.

Over winter nearly all the leaves are dropped; new buds begin to swell under the snow in late spring, an observation made also on V. myrtillus in Finland (Havas 1971). The buds begin to open within a few days following snow release. From each bud a new branch develops, with several leaves and perhaps a few flowers. The flowers begin to bloom as the leaves are still expanding. In the fall the leaves drop, but the new twig formed that spring remains. Axillary buds along this new branch repeat this process the following spring. Further studies on the phenology of V. scoparium are reported elsewhere in this paper.

Vaccinium scoparium is greatly decreased or eliminated from areas receiving trampling. The stems are relatively brittle and foot paths with no Vaccinium shoots were established in less than one season in some of our intensively studied stands.

One conclusion which can be drawn from our observations is the high degree of similarity between V. scroparium and V. myrtillus. Janke (1968) reported similar results from his qualitative observations on V. myrtillus in Colorado. For example, the altitudinal range of V. myrtillus in the Front Range is also 2400 to 3330 m; at timberline V. myrtillus also was found to the lee of krummholz islands; and at higher elevations rings of exceptionally good growth also were often noted around tree boles. The rooting depth, general growth form and phenology of V. myrtillus closely resembles that of V. scoparium. We emphasize these similarities because extrapolations from V. myrtillus to V. scoparium and vice versa, may be useful.

Abundance as affected by late-lying snow.

On July 6, 1973 stakes were driven about the perimeter of snowbanks remaining in the study area on that date (Fig. 36). All of these banks were gone between July 14 and 18. One-half-meter-square circular quadrats were randomly located on zones inside, at the margins, and outside areas snow covered on July 6. The Vaccinium shoots were clipped after the current seasons growth was complete (August 14-21). That year's new leaves and twigs were removed and served as an estimate of that

season's above-ground net primary production. The density of shoots was also recorded in the three zones. All material was oven-dried to a constant weight at approximately 90°C. Dry weights of older stems are expressed to the nearest gram; dry weights of current twigs and leaves were recorded to the nearest hundredth of a gram.

It was also of interest to determine the effect of prolonged snow duration on plants which would ordinarily be released from snow at an earlier date. Three 1 meter-square experimental plots were located, and snow was maintained on these plots for an additional 15-21 days by shoveling snow onto the plots. In this experiment we could judge what effect this lengthened snow cover period would have on V. scoparium shoots found within the plots. After the snow melted from the plots, observations were made periodically on the general condition and phenology of the plants.

Results. Table 43 and Fig. 37 summarize the results. Shoot density, total biomass and net primary productivity were all found to decrease significantly with later snow release.

Billings and Bliss (1959) studied the effect of time of snow release on alpine vegetation in the Medicine Bows, and concluded that the production of several alpine species was dramatically reduced if snow release came after mid-to late-July. Janke (1968) made a similar investigation into the relationship between snow release time and the standing crop, productivity and density of V. myrtillus. He concluded that productivity, density and standing crop progressively decreased if snow release came after June 10. Janke's data are shown in Table 43. The response of V. myrtillus to late snow release appears to be very similar to the response detected in V. scoparium. Dahl (1956), working in the Rondane Mountains of Norway, also commented on the decreasing abundance of V. myrtillus with later snow release. Bock (1971) and Owen (1971) noted lower productivity in subalpine grasses when snow release was later.

Observations on plants within the experimental snow plots revealed no obvious effect of snow duration on the vigor or abundance of the V. scoparium after one year. This may have been because spring

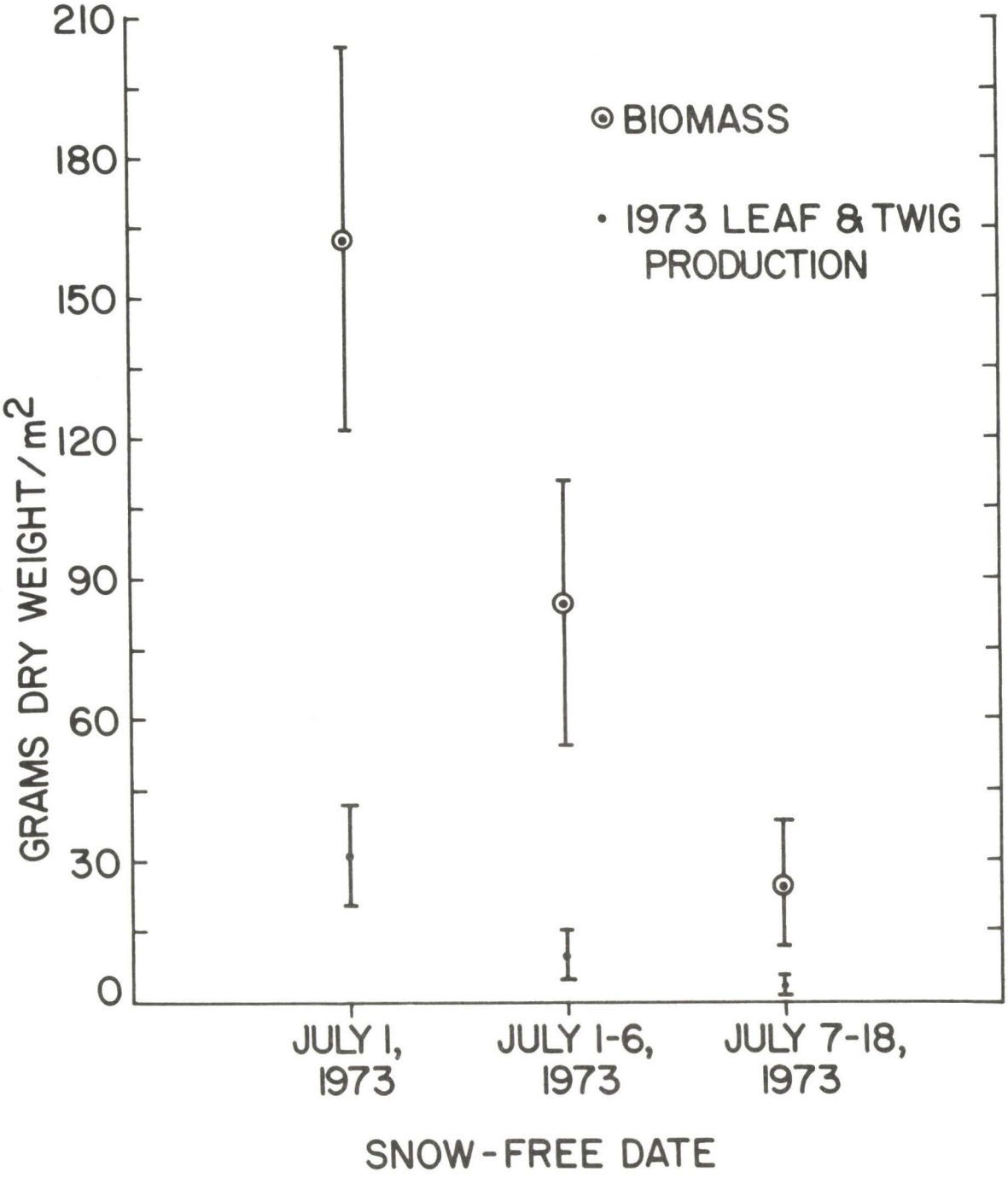

Fig. 37. Biomass and leaf and new twig production of Vaccinium scoparium in relation to snow-free date. Vertical lines indicate the 95 percent confidence interval.

TABLE 43. Biomass, density, and current twig and leaf productivity for *Vaccinium scoparium* and *Vaccinium myrtillus* in relation to snow duration.

Snow Release Date	Above-ground biomass (g/m^2)	Density (shoots/m^2)	Annual above-ground productivity (g/m^2)	Mean shoot productivity (g)
V. scoparium				
Before July 1	164.5	317	32.3	0.102
July 1-6	86.6	222	11.7	0.057
July 7-18	26.0	137	3.7	0.026
V. myrtillus[a]				
Before July 1	38.9	390	28.9	0.074
July 1-8	72.1	388	27.3	0.070
July 8-15	2.0	25	1.3	0.055
July 15-22	1.0	18	0.6	0.036

[a] Data for *V. myrtillus* are from Janke (1968).

shoot growth depends largely on food reserves stored in previous years (Kozlowski and Keller 1966). Four additional plots were established in 1974, and snow will be maintained on these for an extra two weeks during several consecutive years to determine if a long-term shortening of the growing season will affect the plants.

Carbon Budget Studies

As Mooney (1972) states, "Carbon is the vehicle by which organisms store and transfer energy by chemical binding." Atmospheric carbon, in the form of CO_2, diffuses into the plant primarily through leaf stomata, then throughout the intercellular spaces within the mesophyll, and finally into the mesophyll cells to the chloroplasts where carboxylation occurs. The rates at which various plants can fix carbon varies with light intensity, temperature, the photosynthetic pathway, the amount of carboxylating enzyme and plant morphology. Mooney also writes,

> "It is likely that through a quantitative understanding of how different plants gain and allocate their resources it will be possible to make predictions as to their success in any given physical environment..." (Mooney, 1972. p. 315)

Therefore, if shortness of growing season is the factor causing reduced abundance of V. scoparium under areas of late-lying snow, it should be possible to construct a simplified carbon balance model which would demonstrate the length of growing season required by a plant in order to have sufficient carbon uptake for the following years root, leaf, and stem production.

Methods.[1] Respiration and carbon uptake data were gathered in the field and laboratory by means of a mobile gas exchange laboratory similar to that described by Mooney, et al. (1970). Basically this measuring apparatus consists of a temperature-controlled chamber

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[1] We are particularly grateful to A. T. Harrison for his assistance on the gas exchange study. Consult Kyte (1975) for the details of the methods and results on the carbon budget of Vaccinium scoparium.

through which a stream of air is circulated. The intact branch to be studied is sealed into this chamber, and CO_2 in the airstream is sampled before and after passing over the plant by means of a Beckman infrared gas analyser. Differences in CO_2 between the incoming and outgoing air are recorded. Leaf temperature, photosynthetic area or plant dry weight, rate of airflow through the system and amount of light incident on the plant are measured, and the differential in the CO_2 in the airstream is used to compute the CO_2 uptake or loss by the plant on a photosynthetic area or dry weight basis. Leaf and air temperatures are measured with thermocouples, and automatic regulation of leaf or chamber air temperature is provided. Humidity within the system may also be controlled.

The carbon uptake response of the plant to light was determined by holding leaf temperature constant and varying the light intensity by placing neutral density filters over the chamber and measuring the change in CO_2 differential. The carbon uptake or loss by the plant in response to temperature was determined by maintaining light at a level saturating to photosynthesis and by varying the temperature of the plant by means of a cold water circulating system which controls chamber temperature.

Some data were collected on in situ plants in the Mountains, while other data were obtained from plants brought into the laboratory. For example, some plants were dug from under 1.3 m of snow in the spring of 1974, kept in a dark refrigerator at $5^{\circ}C$ for 2 nights, and then observed for several days for CO_2 exchange activity (photosynthesis and respiration) with the gas exchange equipment.

In order to determine the significance of the green stems as a mechanism for maintaining a favorable seasonal carbon balance, CO_2 exchange was observed before leaves were produced, and also before and after removing leaves from the experimental plants.

Results. The results for Vaccinium scoparium can be summarized as follows (see Kyte (1975) for a more detailed presentation):

1. Respiration under the snow at approximately $0^{\circ}C$ probably occurs at the rate of about 0.15 $mgCO_2/hr/gm$ dry weight.

After 7 days of exposure to 13°C temperatures and with the buds beginning to swell, respiration ranged from 0.25 $mgCO_2$/hr/gm dry weight at 5°C to 0.9 $mgCO_2$/hr/gm dry weight at 25°C. Seasonal trends in respiration rate are shown in Fig. 38. Havas and Maenpaa (1972) found that plants of V. myrtillus had the lowest respiration rates in winter, spring rates were highest, and summer-fall rates intermediate. This relationship was not found for V. scoparium, perhaps because spring data were gathered only during bud swell, not during leaf and stem elongation.

2. The green stems of V. scoparium are capable of net CO_2 uptake almost immediately following snow release (line A., Fig. 38). Havas (1971) and Havas and Maenpaa (1972) suggest that winter photosynthesis of V. myrtillus under a thin snow cover may be possible. Pisek et al. (1967) report a net positive CO_2 uptake by V. myrtillus and V. vitis-idaea at -3 to -5°C, indicating that the near 0°C temperature under snow would not preclude photosynthesis. The rate of CO_2 uptake increased after acclimation to higher temperatures (13°C). Photosynthesis by green stems at low temperatures soon after snow release, and before leaf production, appears to be an adaptation to a short growing season.
3. V. scoparium is photosaturated at about 7.5 percent of full sunlight in the summer, indicating that light is limiting probably only in the more dense stands of spruce-fir forest, or during heavily overcast days.
4. Approximately 60 percent of the total, green photosynthetic area of a plant shoot is stem. Our data suggest that stems contribute approximately 45 percent of the total amount of CO_2 fixed during the growing season.
5. Seasonal trends of V. scoparium CO_2 uptake at light saturation are shown in Fig. 38. Immediately after snow release the green stems can take up CO_2 at very low rates (Fig. 38, curve A). After a short period of acclimation to light and

above freezing temperatures, the green stems can take up CO_2 at somewhat higher rates (curve B). The highest rates of CO_2 uptake occur during the summer after leaf expansion and twig elongation is complete (Fig. 38, curve C). During late summer and early fall, CO_2 uptake is at a lower rate than in the summer at any given temperature (Fig. 38, curve D_1). This fact, and the lower late summer-fall light response curve, indicate that the photosynthetic apparatus in V. scoparium has been altered in some way so that higher rates of carbon fixation are no longer possible. It is logical to assume that this lowered CO_2 uptake capacity is due to the effect of the below freezing nighttime and lower daytime temperatures which begin to occur early in September in the Medicine Bow Mountains. Havas (1971) states that in summer shoots of V. myrtillus are damaged by temperatures of near $-10^{o}C$. If V. scoparium responds similarly, frost damage and natural senescence of the deciduous leaves may explain the observed lower fall photosynthetic capacity. Curve D_2 (Fig. 38) shows fall CO_2 uptake rates by stems alone after all leaves were removed. As shown in Fig. 38 (lines D_2 and C_2), carbon gain by the green photosynthesizing stems alone is important for increasing the carbon gain of the plants. If lower temperatures cause deactivation of the photosynthetic apparatus during late fall, then curve D_2 may overestimate fall photosynthesis by stems, as this curve was obtained somewhat before leaf drop and before severe freezing temperatures occurred later in the fall.

Discussion. In summary, physiological adaptations of V. scoparium suggest that length of growing season is a critical limiting factor, and that natural selection has led to the evolution of adaptations to minimize survival problems for the species under conditions of short growing season. The green stems are probably adaptive in two ways, 1) they reduce the amount of new photosynthetic area that must be produced each spring by the deciduous species from stored

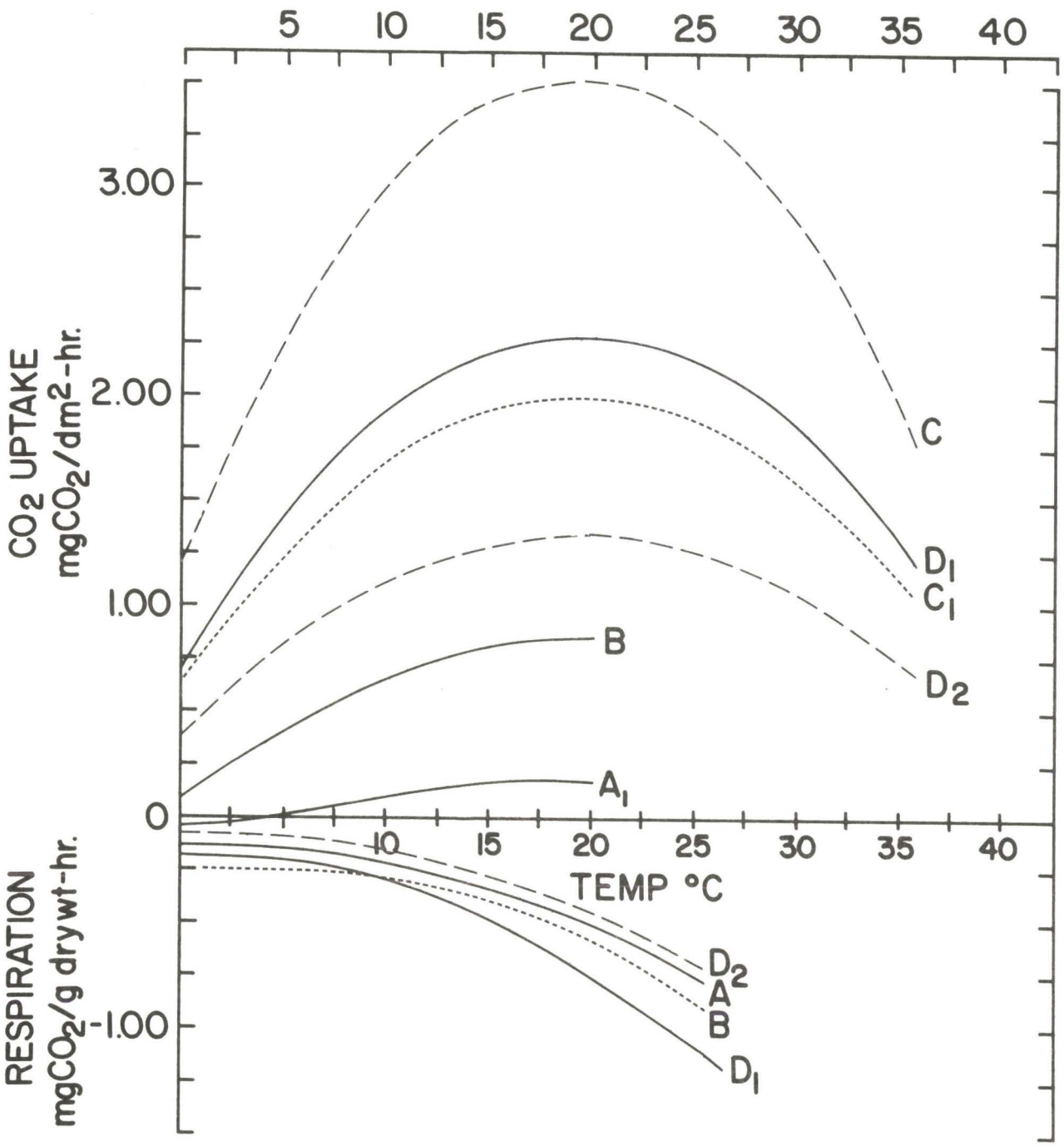

Fig. 38. Seasonal trends of Vaccinium scoparium CO_2 uptake (at light saturation) and respiration in relation to temperature. The lines are lettered as follows: A, winter; A_1, just after snowmelt; B, spring, no leaves; C, summer with leaves; C_1, summer, no leaves; D_1, late summer-early fall with leaves; D_2, late summer-early fall, no leaves.

carbohydrate,and 2) they make a significant contribution to total annual photosynthesis while the plant is leafless during each spring and late fall. The fact that many species have winter-green leaves at higher elevations in the Rocky Mountains (Bell 1974), thereby maximizing growing season length in a similar manner as green stems, further suggests the importance of growing season length as a limiting factor. A shortening of the growing season by more than a few days on a regular annual basis, by whatever means, could be to the detriment of more than a few species. Since maximum snow cover during naturally heavy snowfall years will presumably not be increased by cloud-seeding, we again must ask about the significance to the plants of periodic low snowfall years, or perhaps more correctly, the significance of periodic years when snow cover ablates earlier than usual. The following discussion provides some insight into this question.

An annual carbon budget for V. scoparium was estimated using the data in Fig. 38 in conjunction with measurements of the following:

1. the average length of daylight and dark periods during consecutive intervals throughout the growing season,
2. length of the growing season (days),
3. average day and night air temperatures during consecutive intervals throughout the growing season,
4. leaf and stem surface area per m^2 at consecutive time intervals, and
5. leaf, stem, and root dry weight per m^2 at consecutive time intervals.

We assumed that light is never limiting (which is reasonable because of the low level of photosaturation), that root tissue respires at the same rate as stem tissue, and that the temperature dependence for summer respiration rates is the same as for fall respiration rates.

The CO_2 uptake for a given time period was calculated as follows: length of photoperiod (hrs) x CO_2 uptake rate (mg CO_2/dm^2-hr) x photosynthetic area (dm^2) = mg CO_2 uptake during the light period. The CO_2 lost through respiration was calculated as follows: length of the dark period (hrs) x respiration rate (mg CO_2/g dry wt-hr) x

plant tissue dry wt (g) = mg CO_2 lost during the period. The seasonal CO_2 uptake by leaves and green stems, and the seasonal CO_2 lost through respiration by leaves, stems and roots were calculated separately. The total amount of carbon uptake for the year, minus the total amount of carbon respired during the year, equals the net carbon uptake for the plant that year. If the net annual carbon uptake is multiplied by 0.62, an estimate of net annual productivity (g/m^2) is obtained (Mooney 1972).

Our estimates of the net annual carbon uptake for V. scoparium for 1972 on a meter-square ground area basis are as follows: 118 day growing season (24 June - 19 Oct), 76 g/m^2; 111 day growing season (1 July - 19 Oct), 42 g/m^2; and 104 day growing season (8 July - 19 October), 5 g/m^2. The results suggest that V. scoparium has an annual carbon gain (or positive yearly carbon balance) only if the growing season is long enough, and by extrapolation it appears that a negative carbon balance occurs if the growing season is shorter than about 100 days. Assuming that the growing season ends about October 19, based on our qualitative observations in 1973, the growing season must begin by about July 12 in order for V. scoparium to avoid a carbon loss. No plant can tolerate several consecutive years of net carbon loss. Unfortunately for attempts to determine the effect of snow duration, the 12 July date is not fixed because the end of the growing season will vary from year to year. We hope to develop a mathematical computer model that would allow us to predict the effect on V. scoparium of various annual sequences of different beginning and ending dates for the growing season.

It's clear from our experiment that one year of prolonged snow cover will not kill a plant of V. scoparium. This is no doubt due to the fact that the current year's growth (above-ground), which occurs in approximately 3 weeks, relies upon carbohydrates stored during the previous growing season. It is reasonable to predict for V. scoparium that if the previous growing season was around 100 days or less, a reduced amount of the growth would occur in the current season and no growth would occur after several 100-day growing seasons. Our planned

snow duration experiment will test this hypothesis.

Assuming that the 60:40 root-shoot ratio of V. myrtillus (Janke 1968) is the same for V. scoparium, and that very little browsing of V. scoparium shoots occurs, it is reasonable to assume that about 40 percent of the carbon gained during a growing season goes into new above-ground growth the following year. Therefore, multiplying the net carbon gains obtained during 1972 by 0.40 provides an estimate of the 1973 above-ground productivity based on gas exchange measurements. These predicted above-ground productivity values for different length growing seasons in 1973 are 118 days, 30.4 g/m^2; 111 days, 16.8 g/m^2; and 104 days, 2.0 g/m^2; and are very similar to the actual above-ground estimates obtained in 1973 by sampling, Table 43. The observed new leaf and twig production for 1973 decreased by 1.7 g/m^2 for each day the growing season was shortened by long-lasting snow, i.e., above-ground production was reduced by about 5 percent for each day the growing season was shortened. Total production, as predicted from the carbon balance calculations, decreased by about 5.25 g/m^2-day, or by about 7 percent per day. The fact that these two estimates are so close further suggests that growing season length is the critical factor affected by snow cover, rather than increased soil moisture, different nutrient availability, increased susceptibility to parasites, or some other factor.

Though preliminary, these data on net annual carbon uptake in relation to length of growing illustrate 1) the significance of growing season length to V. scoparium, and 2) how the sequencing of growing season lengths is important to a perennial, semi-evergreen plant's survival. Two or three short growing seasons may not cause the demise of a plant if the fourth growing season is sufficiently long to allow a larger than normal carbon uptake, sufficient to sustain the plants for another year or two of short growing seasons. We wonder how many other plants, and perhaps animals, depend on the same phenomenon.

As discussed before, the question comes back to whether growing season will in fact be shortened by winter snowpack augmentation. On the basis of information now available, it seems unlikely that the area of V. scoparium cover would be reduced by more than a few percent,

namely around the edges of the snowbanks still remaining in early to mid-July (see discussion on pages 189 to 190).

V. Plant Phenology in Relation to Snow Duration

Plants initiate growth, grow to maturity, flower, set seed, produce new vegetative sprouts, and become dormant before beginning the same processes again the following year in temperate regions. All of these events (phenophases) are important to the survival of the species, and their timing (phenology) is of considerable significance. It is reasonable to suspect that longer snow duration might alter the phenology of one or several species in the Medicine Bow Mountains, and therefore we have made a variety of phenological observations during the 3 growing seasons that our research was in progress. We do not necessarily assume that a phenological alteration would be undesirable, but it must be remembered that over a period of thousands of years the plants have been adapting to their environment through evolution. The sequencing of important events is a critical part of the complex of adaptations, and prolonged snow duration may alter that sequence, or at least the time required between important events. If undesirable phenological changes are brought about, a species could 1) survive anyway by evolving new adaptations, or 2) become less abundant. Because prolonged snow duration will probably be localized in snowbanks, if it occurs at all, it is unlikely that any species will be driven to extinction.

Methods for making phenological observations are relatively simple, though some studies become very complex because of the number of growth stages that are observed. The procedure is to mark individual plants and then observe the plants periodically, recording the date that certain events occur. Such data are then compared to environmental changes that occur during the period. In our case, we observed the following for several common species in relation to snowcover duration: 1) initiation of growth (sprouting or bud swelling), 2) length of period for maximum growth, and 3) flowering.

Results

Observations on the meadow species at Headquarters Park indicate that long-lasting snow postpones the initiation of growth and flowering of early flowering species, as suspected, but that the delayed plants often tend to catch up with those that begin earlier (Starr 1974). Billings and Bliss (1959), Bock (1971), and Owen (1971) made similar observations, but found that the net annual productivity of the delayed plants could be reduced. The mechanism for the condensing of phenological events is not well understood, though photoperiod is probably a major factor. Starr (1974) did not find a correlation in Headquarters Park between the beginning or end of flowering and soil temperature or moisture.

We also observed the early phenology of Vaccinium scoparium in several forests at different elevations. Since reproduction is primarily vegetative (no seedlings were found), observations on later phenophases were not made, such as time to fruit maturity. Seven plants at the margin of a naturally occurring snow drift were cleared of a few inches of snow and marked with aluminum tags. The condition of the buds at this time was noted and periodic observations then were made on the state of leaf expansion and twig elongation. Three plants adjacent to each of three meter-square experimental plots were cleared of a few decimeters of snow and observed in the same way. Snow cover was maintained on these experimental plots by shoveling for an additional 15 to 21 days. Three plants from within each of the experimental plots were tagged the day the plants were snowfree. The state of leaf expansion and twig elongation was recorded.

The results for Vaccinium scoparium are presented in Table 44. Approximately sixteen days were required for full leaf expansion and twig elongation at the upper site (3,050 m) during the 1973 season. Artificially prolonging the snow duration from 15 to 21 days had no apparent effect on the time required for full development of new leaves and stems.

Other observations made at lower elevations (2,880 m) during the late spring of 1972 indicated that about 14 days following snow release

were needed for bud burst to occur, and about 24 days were required for complete elongation and foliation. Snow release on that site came on about June 10. Janke (1968) noted that phenological events were accelerated for Vaccinium myrtillus when growth was initiated later in the season. He recorded a 90 day interval from bud burst to mature fruits when bud burst occurred on June 8, but fruit maturation occurred after only 74 days if bud burst occurred on June 30. Gorchakovskii and Shiyatov (1971) presented data on the length of various phenophases for Vaccinium uliginosum in the Polar Urals in relation to the thickness of snow cover, and concluded that with deeper (later melting) snow all phenophases are condensed. Pond and Smith (1971) found that higher elevation Idaho fescue meadows initiated growth later than lower elevation stands in the Big Horn Mountains of Wyoming, but that plants at the higher elevations tend to "catch-up" as the season advances.

The length of the growing season is inversely proportional to the period of snow cover, since the end of the growing season is probably the same for many species (Weaver 1974). Thus a beneficial adaptation to a shorter growing season would be to reach reproductive and/or full photosynthetic capacity more rapidly, i.e., condensation of the phenophases. Apparently this is what happens in a variety of species. We do not know whether this condensation of phenophases is genetically or environmentally controlled, nor do we know if phenophase condensation is to the detriment of the plants involved. On the basis of work done by Billings and Bliss (1959), condensation of phenophases does lead to a decline in annual productivity.

TABLE 44. Phenology of Vaccinium scoparium in the spruce-fir study area (3050 m) in relation to snow duration.

State of buds, leaf expansion, twig elongation	Adjacent to drift		Adjacent to Experimental plots		Within snowbank 1 and 2		Within snowbank 3	
	Date	No. days Snowfree	Date	No. days Snowfree	Date	No. days Snowfree	Date	No. days Snowfree
Buds swelling			7-6-73	0	7-20-73	0	7-26-73	0
Buds opening	7-6-73	0	7-8-73	3	7-22-73	3	7-28-73	3
Leaves expanding, Twigs elongating	7-11 to 7-20-73	6 - 15	7-11 to 7-20-73	6 - 15	7-24 to 8-4-73	5 - 16	7-31 to 8-10-73	6 - 16
Leaf expansion and Twig elongation Complete	7-21-73	16	7-21-73	16	8-5-73	17	8-11-73	17

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THE EFFECT OF SNOW ACCUMULATION ON LITTER DECOMPOSITION AND NUTRIENT LEACHING

D. H. Knight and C. R. Kyte

The litter-decomposer environment is very different when snow is on the ground, being constantly cold (ca. freezing) and moist with little or no diurnal variation. After snow melt the litter dries rapidly, with only irregular and infrequent wetting by summer showers; the temperature is warmer but fluctuates dramatically with exposure to direct sunlight.

Although it seems reasonable to think that most litter decomposition would occur at warmer temperatures, Bleak (1970) and Stark (1972) found that considerable decomposition of plant material could occur under snow in western mountain ecosystems, and Stark (1972) reports that most of the cell content and nitrogen and phosphorous are removed from fresh pine litter during the first winter under snow. Thus, there is reason to suspect that prolonged snow cover would affect annual decomposition rates.

Nutrients released during decomposition may be lost from an ecosystem through leaching, a phenomenon governed in part by the amount of water moving through the litter and soil. During heavy snowfall years there may be more leaching and this could affect plant growth if nutrients are already limiting. Since winter precipitation management is intended to increase snow water on the mountains, will leaching of nutrients increase? Will the rate of eutrophication increase with cloud seeding, especially when combined with the intensive timber management now practiced in portions of the mountains?

The effect of increased snow on decomposition and leaching was studied by means of a simple, small-scale experiment involving a snow treatment. Two null hypotheses were tested:

1. Longer persisting snow will not affect total annual litter decomposition.

2. Increased snow will not promote an increased nutrient concentration in the soil leachate.

The decomposition hypothesis was tested in a spruce-fir forest, a lodgepole pine forest, and a mesic meadow, while the leaching hypothesis was tested only in the 2 forest stands. The 3 study areas are all above 2750 m and are located near Headquarters Park on the western slopes of Medicine Bow Peak. With the time and funds available, we were unable to obtain data on leachate volume and therefore we could not estimate nutrient loss.

Methods

Jordan tension-free lysimeters (Jordan 1968) were installed in each of the two forest ecosystems (2 per pit, 4 pits per ecosystem) in order to evaluate leaching. Installation required first the digging of pits approximately 0.6 x 1 x 1 m deep. Two tunnels with nearly flat tops were dug just below the major rooting zone, with dimensions of about 20 cm diameter by 38 cm long. The lysimeter trough was then firmly wedged against the tunnel ceiling. Water that percolates through the soil over the lysimeter is collected in the trough, where it then flows through rubber hose to a one gallon plastic bottle in the bottom of the pit. The pits were covered during the winter and the only source of water in the bottles was via the soil and collection trough. The water in the bottles was collected once in the spring and tested for nutrient content by the Wyoming State Chemistry Laboratory.

Litter bags (15 x 15 cm) made from 2 mm nylon mesh were used to estimate decomposition rate (Witkamp and Olson 1963). Five bags with Whatman No. 1 filter paper (a cellulose substrate) and 5 bags with litter from the site were placed near each of the 12 pits, for a total of 40 bags in each ecosystem. Meadow litter consisted of dried current growth, while the forest litter consisted of the partially decomposed, compacted fermentation and humus layers on the soil surface. The meadow bags were placed on the soil surface in the meadow from which the litter came; the forest bags were placed in slight depressions in the forest from which the litter was collected in order to simulate the original position of the litter. All bags were weighed (dry weight) before being placed in

the field on October 14, 1972, and again after collection. Half of the bags were collected in the spring whenever the bags became snow-free, and half in the fall on September 15, 1973.

In the meadow ecosystem, 5 of the 10 plots were subjected to a snow treatment, with the other 5 (randomly selected) serving as controls. The snow treatment consisted of adding additional snow by shovel so that snow persisted for approximately 10 days longer than on the control plots.

In the forest ecosystems it was possible to identify patches of ground where snow regularly persists longer, due either to irregular snow accumulation or irregular snow melt. This patchiness became evident through monitoring patterns of snow melt during 1972 and then observing that the vegetation was in fact different under longer persisting banks. Thus, a natural experiment is in process. Two of the pits were dug where banks are known to persist, thereby providing a natural snow treatment, and two pits were dug where snow usually melts about 2 weeks earlier.

Results[1]

Decomposition

The meadow and forest litter bag data suggest that between 70 and 80 percent of the annual decomposition occurs in the winter under snow, which is comparable to the 80 percent figure estimated by Stark (1972) for a Jeffrey pine forest in Nevada. The data for the decomposition of paper were more variable with from 26 to 95 percent of the decomposition occurring under snow (lodgepole forest 26%, spruce-fir forest 69%, meadow 95%). The snow-covered soil was not frozen, but had a surface temperature near 0°C.

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[1] This Project was one of several that had to be curtailed due to the budgetary restriction imposed in 1973. Thus, the sample size is smaller than we had planned and the results are tentative.

TABLE 45. Litter and paper decomposition during the winter, in relation to snow duration. Each value indicates the percent of the original weight that was lost during the winter.

	Lodgepole Forest		Spruce-Fir Forest		Meadow	
Snow-duration	Litter	Paper	Litter	Paper	Litter	Paper
Snow-free early	9.3	7.0	7.7	5.5	39.1	100.0
	10.6	3.3	7.4	6.9	23.8	81.0
	9.2	15.3	6.3	13.8	42.9	100.0
		46.9	7.1	14.9		100.0
		5.2	6.1	16.6		
		9.2	5.9	33.1		
Mean	9.7	14.5 (8.0)*	6.8	15.1	35.3	95.3
Snow-free late	6.5	11.1	9.6	10.7	42.9	78.4
	5.9	5.0	5.4	43.5	41.4	93.0
	6.3	9.9	6.8	88.3	41.8	87.0
	5.7	1.3	6.4	87.2	46.9	100.0
	6.6	5.9	5.4	85.2	39.4	
	5.8	7.6	7.1	59.0		
Mean	6.1	8.2	6.8	62.3	42.5	89.6

* Calculated omitting the very high 46.9 value, which might be the result of an error.

TABLE 46. Mean values for various characteristics of snow water, leachate, and stream water.

Characteristic	Snow-Water	Lodgepole Forest Leachate		Spruce-Fir Forest Leachate		Stream Water
		Snow-free Early	Snow-free Late	Snow-free Early	Snow-free Late	
pH	5.80	6.15	6.20	6.13	6.45	6.70
Conductance (umhos)	6.51	19.25	15.56	15.00	14.00	13.00
Cations (meq/l)	0.10	0.22	0.16	0.16	0.12	0.12
Anions (meq/l)	0.09	0.21	0.14	0.14	0.13	0.11
Ca (ppm)	0.37	2.28	1.50	1.43	1.70	1.40
Mg (ppm)	0.64	0.63	0.30	0.58	0.23	0.35
Na (ppm)	0.43	0.80	1.10	0.40	0.35	0.60
K (ppm)	0.49	0.85	0.73	0.52	0.15	0.20
$-HCO_3$ (ppm)	3.18	4.75	3.90	4.30	4.60	6.70
$-SO_2$ (ppm)	1.63	3.08	0.53	1.50	0.60	0.00
$-NO_3$ (ppm)	0.37	0.50	0.33	0.63	0.58	0.25
Total N (ppm)	1.23	0.35	0.40	0.40	0.20	0.10
Ortho P (ppm)	0.03	0.22	0.13	0.12	0.07	0.04
Fe (ppm)	0.15	0.09	0.08	0.19	0.15	0.05
Si (ppm)	0.06	1.88	1.53	2.80	2.78	4.10

Table 45 shows that, with one exception, the snow treatment had very little effect, if any, on decomposition. The exception pertains to paper decomposition in the spruce-fir forest where a 62 percent weight loss occurred under the late lying snow compared to a 15 percent loss where snow was gone about 2 weeks earlier. Since the natural spruce-fir litter had the same winter weight loss (6.8%) in both areas, the data suggest that the decomposers in the litter where snow persists longer are different species that are better adapted for the decomposition of the paper substrate.

Table 45 shows that the meadow litter decomposed more rapidly than the forest litter. This is probably true, but it must be remembered that current growth was placed in the meadow litter bags while partially decomposed humus was placed in the forest litter bags. It is known that the decomposition of new litter is more rapid than the decomposition of older litter.

Leaching

Table 46 presents data on the chemical composition of old snow, soil leachate from both the spruce-fir forest and the lodgepole pine forest, and water from two nearby streams. As expected, various elements are dissolved in the snow water as it moves through the soil, raising the mean conductance from about 6.5 to an average of about 15 umhos. The only element that appears to be significantly higher in the snow is total nitrogen (Kjeldahl Method). The pH of the snow water is lowest (5.8) and that of the stream water highest (6.7). Our sample was inadequate to detect any significant differences between the spruce-fir forest and the lodgepole pine forest, though the data suggest that the nutrient concentration of leachate is slightly less in the spruce-fir forest.

The leachate from under late-lying snow banks is slightly different in chemical composition than leachate from areas that are snow-free earlier, Table 46. The results suggest that, if anything, less nutrients are being leached from soils with late-persisting snow (and very little live-plant groundcover). The best evidence for this is the data on conductance, total cations and anions, magnesium,

potassium, ortho phosphorus, and sulphate. The sample size was again smaller than anticipated, however, and we would only conclude from these data that a late-lying snow bank is not having a large effect on the nutrient concentration of leachate from the upper 20 to 25 cm of soil. An accurate estimate of nutrient loss would require data on the volume of leachate, data which we were unable to obtain.

Discussion

Our results suggest that both hypotheses can be accepted. We did not observe any significant effect of late-persisting snow on total annual decomposition, nor did we observe an increase in the nutrient concentration of leachate water where snow remained on the ground for 10 to 14 days longer. These results, however, must be placed in proper perspective, and have different meaning depending on whether the data were obtained from the meadow or forest.

In the meadow a new experiment was established, i.e., for the first time in 1973 a certain portion of the meadow had later-persisting snow than the rest of the meadow. New snow banks of about 1.5 to 2 m^2 were created by shovelling. The effect of snow duration alone could be best evaluated in this situation because everything else was very comparable for the treatment and controls; the dominant vascular vegetation was very similar in the paired plots and there is no reason to think that the available decomposers would be different. As the results suggest, there was little or no effect of the new snow banks on litter decomposition (which means weight loss in our study) in the meadow.

Essentially the same conclusion is possible for decomposition in the forest. However, the forest experiment was based on snow banks that had occurred naturally for a sufficiently long time that differences in the ground vegetation were obvious and differences in the decomposers probably existed also. Thus, differences in decomposition cannot be attributed to any one factor; snow duration, ground-cover vegetation, and decomposers could all be involved. The data are relevant, however, because they provide

an indication of the magnitude of future change that might be expected if new snow banks are formed where they do not now occur.

The amount of nutrients in the leachate from under late-persisting snow banks is so similar to the "control" that the differences could easily be due to sampling error, however, the trend is sufficiently consistent to call for a possible explanation. The effect, if it is real, may be more directly related to the near void of vegetation under the persisting snow banks. McColl and Cole (1968) have discussed how elemental leaching in some coniferous forests is partially regulated by the amount of $-HCO_3$ anion, which is partially regulated by the amount of CO_2 production by organisms in the soil. Perhaps the relative lack of vegetation, due possibly to longer snow cover, leads to less CO_2 production and $-HCO_3$ formation, and thereby less potential for leaching. Of course, decomposers and tree roots undoubtedly do exist in the soil and are another source of considerable CO_2.

Two major questions remain to be considered. First, is it reasonable to expect that new snow banks will be formed by cloud-seeding, or that snow duration will be longer as a result of cloud-seeding. Answering these questions requires research of a nature that we did not propose. One study (Progress Report to Bureau of Reclamation for Contract No. 14-06-D-5496, Jan. 1 to June 30, 1971) suggests that a 10 to 15 percent increase in new snow produced by cloud-seeding would melt within 3-5 days of normal, a shortening of the snow-free period by even less than our "snow treatments". Of course, annual fluctuations in snow fall are known to be greater than 100 percent, so the problem becomes one of evaluating what the effect would be of changing the mean time of snow duration in the spring. Our data suggest that the effect will be minor, and also very difficult to measure.

There is, however, a possibility that new snow banks will be formed by the drifting of man-produced snow, so that banks are created in new areas or old banks become larger. Furthermore, it is conceivable that due to drifting a snow bank may be increased in size by 50 or 100 percent even though total snowfall has only been increased by

15 percent. The likelihood of this happening will depend on the aerodynamic characteristics of the surrounding terrain, a subject that was not studied during the Medicine Bow Ecology Project.

The second question relates to whether or not more nutrients will be lost from a watershed if more water passes through the watershed, which is certainly the desired objective of winter cloud-seeding in the Rocky Mountains. In spite of our observation that elemental concentration of leachate is not significantly affected by late-lying snow, an increased elemental loss from the watershed can be expected. Whether this increased loss will be ecologically significant over a short or long period of time is not known. More must be learned about the rate of elemental inputs into Rocky Mountain ecosystems and the extent to which biological activity is limited by nutrients. Some research shows that logging hastens the rate of stream eutrophication. Logging combined with cloud-seeding may increase the rate of eutrophication still more, but this is a question we have not been able to pursue in our research.

Thus, the results of our pilot study contribute toward resolving the bigger question of total effect of winter cloud-seeding on nutrient cycling in the affected watersheds, but they provide no basis alone for evaluating the effect on nutrient cycling.

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THE RELATIONSHIP BETWEEN TROUT ECOLOGY AND ANNUAL SNOWPACK IN THE MEDICINE BOW MOUNTAINS

G. Baxter and J. Loar

An increase in snow can be expected to increase streamflow and decrease stream water temperature. Although increased volume could enhance fish production, lower water temperature may reduce production. The combined effect of lower water temperature and increased volume is not known. Thus, this study was undertaken to examine the relationships between annual snowpack, spring runoff, brook trout production, and trout food production in the Medicine Bow Mountains. Since considerable data are already available on the lake fishery (see pages 85 to 93), this study focuses on streams. Special emphasis is given to the growth of trout at different elevations where temperatures differ, and to the biomass of stream invertebrates. Some of the data presented in this report will serve as a baseline by which to judge the long-term effects of winter cloud seeding (see also page 85).

Study Areas

Data were collected from the following sites (Fig. 39).

1. Nash Fork Creek, 1000 m section at the S. H. Knight Science Camp, R79W-T-16N-S13 and 14, elevation 3078-3100 m.
2. North French Creek, approximately 1500 m section upstream from the bridge crossing on the North French Creek Road, R80W-T16N-S29, elevation 2960-3000 m.
3. Towner Lake and its inlet stream, upstream to the Towner Lake road crossing, R79W-16N-S15, elevation 3200 m.

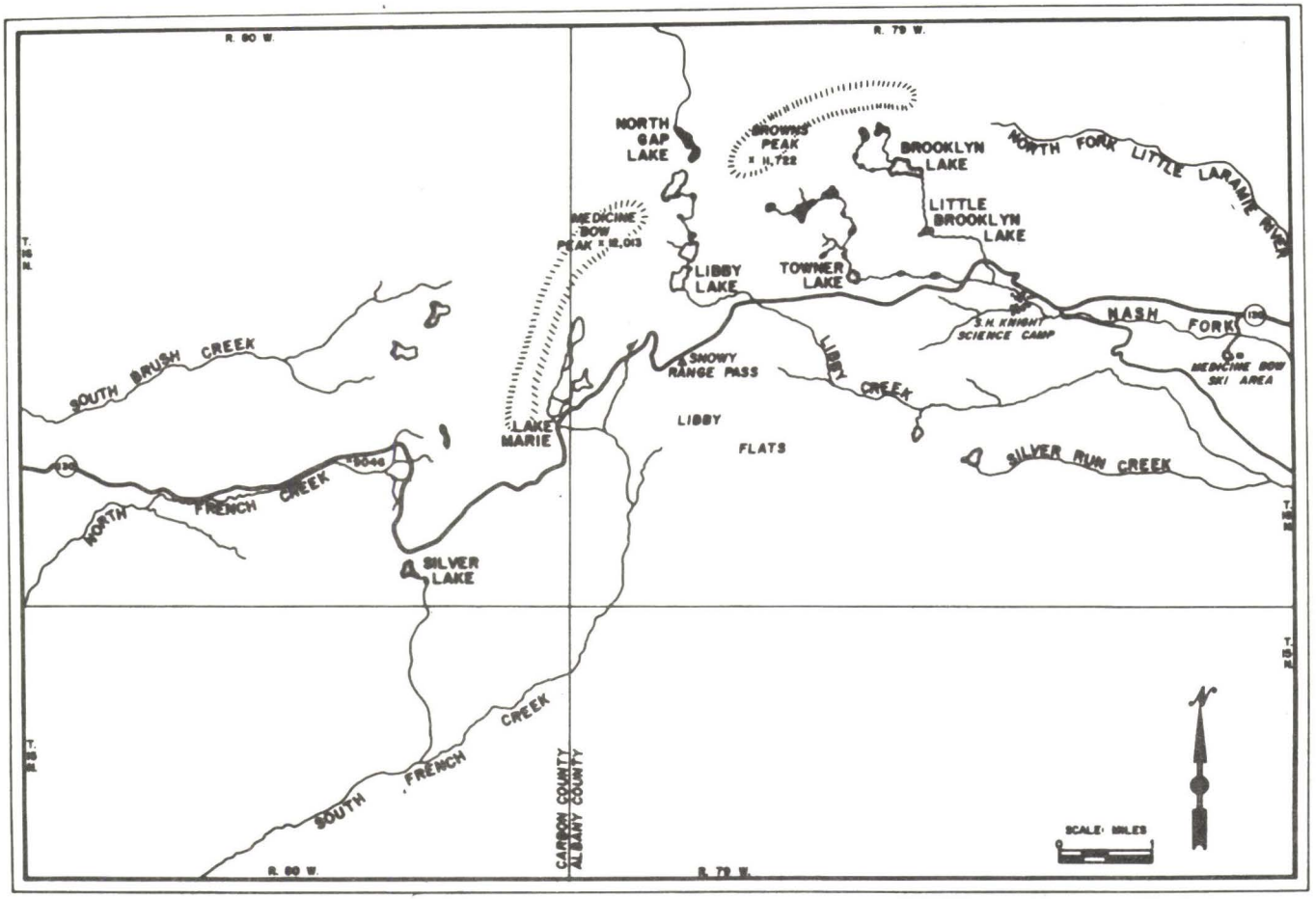

Fig. 39. Map showing the streams and lakes that have been studied in the Medicine Bow Mountains.

4. Libby Lake and its outlet stream, 200 m downstream, R79W-T16N-S17, elevation 3300 m.

Nash Fork Creek at the primary study site is a torrential mountain stream with a July volume flow of about 5 m^3/sec and velocities of as much as 1.5 m/sec. The bottom type in the study area includes bedrock, boulders (32 cm), large rubble (20-32 cm), medium rubble (12-20 cm), small rubble (5-12 cm) and coarse gravel (2-5 cm). The upper end of the section is at the confluence of Nash Fork Creek and Telephone Creek upstream from the S. H. Knight Science Camp. The lower end of the section is marked by the first of a series of beaver dams in the moraine basin below the Science Camp. The stream flows through a mature native forest of mixed Engelmann spruce, subalpine fir, and some lodgepole pine. Streamside vegetation includes willows, bearberry honeysuckle (Lonicera involucrata), and a variety of herbacious plants among which Mertensia sp. and Senecio triangularis are especially conspicuous. The streambed in the study area is 1000 m in length and the mean width, 5.65 m. The gradient of the streambed varies from 31% to as little as 11% at the lower end. Some fish cover is provided by undercut banks and fallen trees but the primary cover is in eddies among large boulders.

In August, 1972, the dissolved oxygen content of the water was 6.5 to 7.1 (different areas), methyl orange alkalinity was 50 ppm, and the pH 7.4.

North French Creek drains the west slope of the Snowy Range with headwaters from the Sucker Lakes and nearby alpine meadows. The stream courses parallel to Highway 130 for several miles before entering a relatively deep canyon and coursing south to join the Middle and South forks. The upper end of the study section is a meandering stream with low velocities and a bottom of sand and small to coarse gravel. The lower half of the section is of steeper gradient with a bottom of rubble. The mean width was 5.06 m and the volume flow was 0.6 m^3/sec (19.5 cfs) on July 10, 1972. The streamside habitat is mostly open meadows with some scattered spruce,

fir and lodgepole pine. Excellent spawning facilities and considerable cover provided by undercut banks results in a dense population of brook trout. Unfortunately the brook trout population was found to be suffering a chronic infection of bacterial kidney disease. Although mortalities and general intensity of infection are low, the precautions required to prevent the spread of this disease complicated the conduct of this study to some extent.

Libby Creek immediately below the outlet of Libby Lake and for approximately 200 m downstream was a site for measurements of water temperatures and growth of brook trout. At this point Libby Creek is a small alpine stream with an average width of about 2 m and a July 1 volume flow of 0.62 m^3/sec (22 cfs). The bottom is mixed gravels and rubble. The meandering stream, interrupted by one deep pool, flows through an alpine meadow.

Towner Lake is a small (3.56 ha) subalpine lake at 3200 m in the Telephone Creek drainage system. It is a natural lake but its depth has been increased by a small man-made dam which is no longer maintained. The maximum depth is about 2 m, the bottom is muck with some boulders. Fairly extensive beds of Elodea develop in the lake in late summer. Earlier studies have described the fishery, which is an important one in this drainage (see pages 85 to 93). The growth of brook trout in the lake and the inlet stream (Telephone Creek) were measured together with water temperatures.

Methods

Weather and streamflow data have been collected since 1965 by the Water Resources Research Institute, University of Wyoming, and were used in our analysis. In addition, water temperatures and, in the summer of 1974, air and water temperatures, were measured at selected locations on Nash Fork, Libby, and North French Creeks by means of Moeller recording thermographs.

Stream invertebrates were sampled using an enclosed sampler fashioned from fiberglass and netting and fitted with a sponge rubber seal. This device samples an area of one-tenth of a square meter. A 480 m section of Nash Fork Creek at the S. H. Knight Science Camp was sampled at various times in 1972 and 1973. Each study station was subdivided (as a means of stratification) and a sampling transect was chosen in each subdivision using a random number table. The study section of Nash Fork Creek was subdivided into 20 twenty-four meter sections. From one to six samples were taken along each transect at varying distances apart as required to avoid overlap, the number depending upon the width of the stream at the transect. If the depth or velocity of the current made sampling impractical at a chosen transect, an alternate sampling location was selected. Samples were preserved in plastic freezer containers in approximately 10% formaldehyde solution and stored for later analysis. Organisms from the samples collected in 1972 and 1973 from Nash Fork Creek and North French Creek were separated from the trash and gravel in the sample by flotation in a mixture of vegetable oil and water. Final separation was carried out under a binocular microscope. In order to compare population numbers with those of Good (1974) which were hand-picked, comparisons are made only between organisms two millimeters or more in length.

Samples of fish for studies of growth were collected by dip-netting, seining, electrofishing and gill netting. In 1972 fry were collected at approximately 3 week intervals from several habitats. In 1973 and 1974 young-of-the-year brook trout were collected from each study station at the end of the growing season.

Population estimates were made using a mark and re-capture technique. Fish were collected by electrofishing, using pulsed direct current delivering approximately 0.5 amperes. The fish were fin-clipped and returned to the stream section from which they were collected and recaptured within three days. Different fin clips were used for different subsections of the streams and this was used as

a check on up- and downstream movement of marked fish during the course of the experiment. The estimate of population size (N) was calculated from N = (M) (C+1)/ (R+1) where M = number marked, C = number examined for marks and R = recoveries. Confidence limits were calculated by treating R as a Poisson variable (Ricker 1958).

Measurements of downstream drift of stream invertebrates were made in connection with food studies by anchoring a 30 x 30 cm net in the stream for 30 minutes or, in some daylight samples, for one hour.

Collections of fish for stomach analysis were done by electrofishing using pulsed direct current. In 1974 fish were collected at approximately 2 week intervals from mid-July through mid-August. A sampling day was subdivided into four sampling periods between 6 a.m. and 10 p.m. Subsamples of 3 or 4 brown trout and 3 or 4 brook trout, and any rainbow trout collected up to 4, were collected for each sampling period, with ages older than 0+ represented in the proportion they were shocked. Body cavities were incised and the fish preserved in formalin. The contents of each stomach from esophagus to pylorus were measured volumetrically and the contents sorted into taxonomic categories and counted. Numbers of benthic invertebrates were converted to weight units using conversions established by Good (1974).

From the data on numbers and weights of different taxonomic categories in the stomach contents, an importance evaluation similar to the importance value used by plant ecologists (see Whittaker 1970) was calculated using the sum of the percentage of total numbers, percentage frequency and percentage of total wet weight for the major food categories.

Age and growth analyses were made by the scale method. Scales of fish collected at regular intervals in 1972 and at the end of the growing season in 1973 were sampled from 4-5 scale widths above the lateral line at the level of the dorsal fin in order to insure uniformity of size of scales. Wet mounts were photographed and age assessment and measurements from the posterior edge of the focus to

the first strong circulus of each annulus were used for back calculating length-at-age by the direct proportion (Dahl-Lea) method or in some cases by the Fraser method (Carlander 1969, p. 15). In most cases 4 scales from each fish were measured and the mean dimensions used for the back-calculation of length at age.

Major limitations of methods for collection and analysis of data are considered to be as follows:

1. Some temperature data are missing due to malfunction of instruments and human disturbance of instruments.
2. Picking and sorting of invertebrates were conducted by several different workers and using several different techniques for separating and sorting. Only data which were considered logically comparable were used for statistical comparisons.
3. Population estimates depend upon the well known assumptions governing the validity of the mark and recapture method (Ricker 1958).
4. Age assessment by the scale method and back-calculation of growth increments in different years from scale measurements is a procedure whose accuracy depends upon correct age assessment from scale markings and uniformity in size and proportions of scales. This method is also subject to the effects of the Rosa Lee phenomenon, where the calculated growth increments of older fish are smaller due probably to selective mortality of faster growing fish in both exploited and unexploited populations.
5. In analysis of fish stomach contents, measurements of the weight or volume of different components of the diet are subject to considerable error due to fragmentation of the stomach contents and the presence of mucous in the stomachs. This error is greatest, of course, in the stomachs of very small fish and when stomachs contain only very small amounts of food.

Results

Growth

Growth of brook and brown trout in streams above 2700 m elevation near the Snowy Range is comparatively slow (Tables 48-49 and Fig. 19). Carlander (1969) lists only one stream habitat (Nova Scotia) which showed growth slower than that in North French Creek, and the growth of brown trout in Nash Fork Creek is comparable to that in "stunted" populations in streams in Scandinavia and Britain (Carlander 1969).

Fish of Age V are very rare in the stream habitat, and age IV fish are not abundant. Among 166 fish whose scales were examined for age assessment in the summers of 1972 and 1973, none were age V and 24 (14%) were age IV; these were collected by electrofishing which is selective for larger and hence older fish. The sample of 34 fish from Towner Lake included 2 (6%) Age V fish.

Food and Feeding

The stomachs of 52 brown trout, 45 brook trout and 23 rainbow trout, of a variety of ages and collected at different time periods, were examined and the contents quantified (see Methods). Stomachs of all species were lumped for the analysis of diet composition. There is no indication of diet differences between the three species in this habitat. If there were a difference it would not affect this analysis, where the principal objective was to determine the importance of the different stream invertebrates in the total diet of the trout population.

Table 48 shows the importance of the different categories of food, including terrestrial organisms, found in the stomachs. This analysis indicates that terrestrial insects (mainly caterpillars, terrestrial Diptera, beetles, ants, and spiders) were the most important food items during the period from July 12 to August 14. Next in importance were mayfly nymphs of the family Baetidae. In Nash Fork Creek three baetids predominated, B. bicaudatus, B. tricaudatus, and B. intermedius. During the period of the food study, B. intermedius

TABLE 47. Total length (mm) and weight (g) at successive ages of trout from 2 streams.

	Brook Trout				Brown Trout	
	Nash Fork Creek		North French Creek		Nash Fork Creek	
Age	L	W*	L	W*	L	W*
0+	69	4.1	55	1.4	66	3.4
I+	112	16.4	96	8.4	125	22.5
II+	150	37.5	130	22.1	166	51.6
III+	178	60.9	155	38.8	205	95.9
IV+	-	-	182	64.9	242	156.1
V+	-	-	-	-	264	201.5

* Calculated from regression of W on L

TABLE 48. Importance value* of major food categories in the stomachs of brook and brown trout from Nash Fork Creek, 1974.

	7-12-74	7-25-74	8-14-74	mean
Nymphs				
Ephemeroptera				
Baetidae	94.5	79.8	79.8	84.7
Ephemerella doddsi	24.1	14.0	2.8	13.6
Heptageniidae	67.9	77.6	58.4	67.9
Plecoptera				
Alloperla spp.	16.7	22.2	26.8	21.9
Acroneuria pacifica	9.35	not present	not present	3.1
Trichoptera				
Rhyacophila spp.	58.3	49.6	80.6	62.8
Arctopsyche spp.	17.8	6.9	17.7	14.1
Glossosoma sp.	not present	not present	79.9	26.6
Diptera				
Chironomidae	68.9	45.3	35.1	49.8
Simuliidae	52.0	26.5	31.3	36.6
Adults				
Ephemeroptera	126.3	26.8	23.6	58.9
Plecoptera	43.9	36.9	37.8	39.6
Tricoptera	37.5	21.9	12.7	24.0
Diptera	-	-	21.8	7.3
Combined Terrestrial Food	113.4	116.00	152.4	127.3

* Calculated as % of numbers plus % of total wet weight plus % frequency.

TABLE 49. Importance* of major taxonomic categories in drift samples (D), benthic samples (B) and stomach contents (S), Nash Fork Creek, 1974.

	7-11-12			7-25-26			8-14-74			Mean		
	D	B	S	D	B	S	D	B	S	D	B	S
Baetidae	149.6	27.3	49.2	132.8	49.7	44.8	146.3	46.3	32.5	142.9	41.1	42.2
Ephemerella doddsi	np**	3.9	19.5	1.6	2.0	11.1	2.4	8.0	2.0	1.33	4.6	10.8
Heptageniidae	36.4	111.5	44.1	34.3	61.4	55.2	11.5	41.6	41.2	27.4	71.5	46.8
Alloperla spp.	1.6	34.5	2.1	3.7	38.7	6.8	1.1	38.1	4.6	2.03	37.1	4.5
Acroneuria pacifica	np**	.5	1.0	np**	.9	np**	.7	5.8	2.5	.2	2.4	1.2
A. signata	np**	1.3	np**	3.1	1.8	np**	np**	4.8	np**	1.0	2.6	np**
Rhyacophila spp.	.9	2.8	33.7	.5	4.4	19.6	3.9	14.9	41.2	1.8	7.9	31.5
Arctopsyche spp.	np**	5.5	7.4	np**	np**	20.1	np**	-	14.8	np**	1.8	14.1
Glossosoma sp.	np**	np**	np**	np**	np**	np**	1.4	6.5	29.3	.5	2.2	10.5
Chironomidae	1.4	4.1	12.7	.8	28.4	15.5	2.8	15.1	10.4	1.7	16.4	12.9
Simuliidae	7.1	.6	10.6	14.0	np**	4.0	13.4	4.5	10.5	11.5	1.7	8.4
Tipulidae	np**	1.9	np**	np**	2.3	np**	np**	np**	np**	np**	np**	

* Calculated as % of total wet weight plus % of total numbers

** not present

made up over 90% of all baetids, but in the partially digested stomach contents the three species could not be distinguished. The baetids were followed, in descending rank of importance, by heptageniid mayfly nymphs (three principal species, Rithrogena brunnea, Epeorus longimanus, and Cinygmula sp.), caddis larvae and pupae of the genus Rhyacophila (at least 5 species), adult mayflies, and then midge larvae and pupae (Chironomidae), including several genera and species.

It is noteworthy that benthic forms (nymphs and larvae) and the surface forms (adult aquatic insects together with the terrestrial forms) were of about equal importance, and that terrestrial organisms increased in importance in the trout diet as the season progressed, while the adults of the aquatic insects decreased. This results from the fact that the peak of emergence of the most important mayflies and stoneflies occurs during early July, tapering off gradually throughout the remainder of the summer. Thus both the large, late-instar nymphs in the benthos and the adult mayflies and stoneflies became much less available by mid-August, and in the last sampling most of the nymphs in the benthos are newly hatched individuals which are too small to be readily captured by the trout. Because Baetis intermedius is a late emerger, replacing the other two species in the benthos in August, baetids remained at about the same level of importance, as did Rhyacophila which is also represented by several species.

The high value of Glossosoma in August is important. This caddis builds a shelter of small gravel on the rubble from which it is presumably ingested by the fish, resulting in stomachs with a large volume of gravel but little in the form of digestible food.

Table 49 shows the relative importance of the different food categories in the drift, the benthos, and the stomach contents. Because the numbers of samples for benthos and drift were small, the value for percentage frequency is not meaningful, so the importance index is simply the sum of per cent of total numbers and per cent of total wet weight. In this analysis, also, the values for the stomach contents do not include the terrestrial organisms nor adult aquatic

insects since these did not appear in benthos samples and were not included in the counts of drift.

In the stomachs, heptageniid nymphs ranked first in importance, followed by baetids and then Rhyacophila sp., and this was paralleled in the benthic samples. In the drift the baetids were first in importance by a large margin. Although it is well known that brook trout and brown trout utilize drift for food (Elliot 1967, Griffith 1974, Horton 1961), it is impossible to ascertain whether aquatic nymphs and larvae in the stomachs were taken from the drift or from the bottom. One important factor is the diel pattern of drift. Baetid nymphs are strong drifters but drift mostly in the hours of darkness. Simulids, on the other hand, are daytime drifters and probably for this reason make up an important part of the diet relative to their abundance in the ecosystem. As has been shown in many studies of trout food, Nash Fork Creek trout are seen to be opportunistic, utilizing a wide variety of foods and, at any given time, concentrating on the food that is abundant and convenient to ingest.

Population estimates

Estimates of population densities, species composition, and standing crop biomass of Age I and older fish were made for the study sections of Nash Fork Creek in 1972 and 1973 and of North French Creek in 1973. These estimates are considered to be quite representative for torrential mountain streams in the area. In Nash Fork Creek, a series of beaver ponds immediately below the study section supports fish populations of an entirely different structure, since such sectors of the stream act as catch basins for drifting fry and fingerlings. For this reason and because the smaller fish were not effectively electrofished in the fast waters of the study sections, the population estimates do not include Age 0 fish and the estimates of Age I fish are low.

The mark-and-recapture data for the two years were used to calculate fish biomass, Table 50. The lower biomass of trout in Nash Fork Creek may be due to any or all of several factors, including the drift of younger fish to the slower water immediately downstream, the more torrential nature of Nash Fork Creek which provides less spawning habitat and causes more downstream drift, and probably some effects of competition between the brook and brown trout. North French Creek is not so torrential and many younger fish remain in the habitat. In this stream, 27% of the fish captured in sections 3 and 4 were Age I fish. In Nash Fork Creek in 1972, only 5% of the fish captured were Age I fish.

Allen (1969) tabulated estimates of stock densities for salmonids in streams. His calculations of densities, expressed as m^2/fish ranged from 2.2 to 120 and a plot of average area per fish against length on a logarithmic scale represented a density of about 17 kg per hectare. By this standard the density of brook trout in North French Creek (1.82 and 3.52 m^2/fish for the upper and lower sections, respectively) would be considered very high and that in Nash Fork (10.9 m^2/fish) above average.

TABLE 50. Trout populations in 2 stream habitats in the Medicine Bow Mountains, estimated using the mark and recapture method.

Habitat	Year	Section	Area m^2	Est. Total No.	Percent Brk/Brn/Rb	Estimated Biomass kg/ha
Nash Fork	1972	1-6	4391	403	55/40/5	78.7
Nash Fork	1973	1	732	54	79/21/0	48.6
	1973	4	732	47	17/79/4	69.7
N. French	1973	3,4	655	719	100/0/0	106
		1,2	655	372	100/0/0	192

Reproduction

An intensive study of spawning activities of the stream-dwelling salmonids was not made, but for brook trout at least, they are not believed to differ substantially from those of the lake fisheries described by Hepworth (1959) and Christensen (1965). In the streams there is some upstream migration of both brook and brown trout but this is partially blocked by water falls or beaver dams and most of the spawning takes place within a few hundred meters of the summer habitat. Spawning takes place from September through November when mean daily water temperatures are below 10°C. The males become ripe earlier than females and brook trout ripen earlier than brown trout.

Estimates of brook trout fecundity were made in 1973 for females collected from Nash Fork Creek and North French Creek. The regression lines for number of eggs (E) on total length were, for Nash Fork Creek, $E = -664.72 + 6.28L$, and for North French Creek, $E = -988.84 \pm 8.62L$. Thus, in Nash Fork Creek, a 230 mm (9") female produced on the average about 780 eggs, and in North French Creek, about 900 eggs.

Movement of Fish

The downstream drift of young brook trout in the streams of the Medicine Bow Mountains is an important factor in their ecology (White 1965). In North French Creek in 1972, an overpour trap which intercepted an estimated half of any fish moving downstream caught a total of 19 fish during the month of August. All these fish were in the size range from 114 mm to 165 mm and were presumed to be Age II fish. Why no Age 0, Age 1 or Age III fish were trapped by the downstream traps is not known. The kidney disease infection in the North French Creek population complicated the study of movement since precautions had to be taken to prevent contamination of equipment and the spread of this disease to other streams. In that same period (August 1972) 22 fish were trapped in the overpour trap in Telephone Creek above Towner Lake. These included two Age I fish, two Age II fish

and sixteen Age III- and-older fish. Overpour traps set in Nash Fork Creek above the principal study area and in Sally Creek during this period caught 2 and 1 fish, respectively. The only conclusion that might be drawn from these limited data is that downstream drift is erratic, may include all size and age classes, and is probably related to population density. A major source of error in our results was the size of our traps, which did not span the entire width of the streams.

Movement of Stream Invertebrates

One primary objective of this study was to determine the influence of increased snowpack on the populations of stream invertebrates which serve as food for trout. The importance of these organisms in the diet of trout has been discussed previously. An increase in the snowpack might reduce these populations, since many of the species would be subjected to downstream and/or habitat displacement as a result of the higher volume flows during the period of snowmelt.

In order to test this hypothesis we first obtained estimates of the population densities of species in the orders Coleoptera, Diptera (excluding the family Chironomidae), Ephemeroptera, Plecoptera, and Tricoptera in Nash Fork Creek at various times in 1970, 1972, and 1973. Sampling dates and the number of samples collected at each time as well as species population densities are given in Table 51. The nonparametric Mann-Whitney U-test was used to analyze differences between years for the more important species and for the total number of organisms found at each sampling period.

The results of the statistical comparisons are given in Table 52. In 1972 samples were taken on May 30-31 during the rising phase of the runoff curve (Fig. 40). Organisms such as Epeorus longimanus, Cinygmula sp., and a portion of the Rithrogena brunnea population are very small at this time and are less able to withstand the higher current velocities. In 1973, on the other hand, the higher volume flows occurred after the first sampling period (May 26, 28).

TABLE 51. Mean number of organisms per one-tenth square meter for each sampling period in 1970, 1972, and 1973 in Nash Fork Creek at the S. H. Knight Science Camp. Values for August in 1972 and 1973 include organisms ≥1 mm in length. All other values are based on organisms ≥2 mm in length.

Species	1970		1972			1973		
	June 2-3 (n=25)	July 27,29 (n=27)	May 30-31 (n=23)	July 16-18 (n=20)	August 17 (n=20)	May 26,28 (n=20)	July 26-27 (n=20)	August 17-18 (n=20)
Ephemeroptera								
Ameletus sp.	0.4	1.0	0.3	0.05	2.2	0.2	0.05	1.1
Baetis bicaudatus	2.7	2.2	39.3	4.2	1.5	25.2	1.3	0.1
Baetis intermedius	0.0	46.7	0.0	58.3	21.8	0.0	27.0	13.6
Baetis tricaudatus	0.2	35.7	1.6	3.2	1.9	0.2	3.5	3.0
Centroptilum sp.	0.0	6.5	0.04	0.6	0.05	0.1	2.4	0.7
Cinygmula sp.	20.3	12.8	47.7	22.2	4.4	73.5	21.4	9.2
Epeorus longimanus	0.8	9.8	1.0(10.2)*	15.9	11.2	1.4(22.0)*	14.2	6.4
Ephemerella coloradensis	0.6	0.6	2.1	0.1	0.0	4.7	0.4	0.6
Ephemerella doddsi	3.0	0.7	6.4	0.9	29.0	11.4	2.6	33.4
Ephemerella inermis	1.1	0.3	2.3	0.5	13.1	1.4	0.2	3.2
Ephemerella margarita	0.0	0.04	0.0	0.0	0.0	0.0	0.2	0.2
Paraleptophlebia sp.	0.6	0.8	0.3	0.6	3.0	0.4	1.8	2.8
Rithrogena brunnea	5.6	7.0	8.3	15.4	45.1	26.2	36.9	48.9
Rithrogena doddsi	0.0	0.0	0.0	0.2	0.05	0.0	0.5	0.1
Plecoptera								
Acroneuria pacifica	0.6	0.8	0.6	0.5	1.6	2.0	2.6	2.0
Alloperla autumna	0.1	0.7	0.0	0.0	0.0	0.5	0.2	0.0
Alloperla borealis	4.4	5.8	5.9	9.9	9.5	8.0	24.8	32.0
Alloperla lambda	1.4	0.1	1.2	0.2	0.0	1.6	0.05	0.0
Alloperla lineosa	0.0	2.2	0.0	6.2	0.4	0.0	2.0	0.6
Unident. Alloperla spp.	4.8	12.4	3.1	6.0	3.8	6.2	7.4	10.4
Arcynopteryx signata	0.2	0.8	0.2	1.4	0.5	0.8	2.2	0.6
Brachyptera nigripens	0.04	0.0	0.0	0.0	0.0	0.4	0.0	0.3
Eucapnopsis brevicauda	4.2	0.0	6.8	0.0	3.4	8.2	0.0	1.7
Isogenus modestus	0.1	0.1	0.2	0.0	0.1	0.3	0.05	0.05
Isoperla fulva	0.4	0.0	0.8	0.0	1.2	1.0	0.05	0.4
Nemoura cinctipes	0.9	0.3	0.3	1.4	0.8	0.4	1.6	2.6
Nemoura delicatula	0.7	0.0	0.3	0.0	0.2	0.6	0.0	1.0

* Value includes individuals less than 2 mm in length.

TABLE 51. (Continued)

Species	1970		1972			1973		
Nemoura hazi	0.0	0.0	0.4	0.1	0.0	0.0	0.0	0.2
Nemoura oregonensis	1.5	1.0	1.6	2.5	2.1	3.5	4.6	6.0
Nemoura sp. 1	0.0	0.0	0.0	0.0	0.0	0.05	0.0	0.0
Paraleuctra occidentalis	0.6	0.4	0.3	1.4	1.8	0.6	2.6	6.4
Paraperla occidentalis	0.0	0.0	0.0	0.05	0.0	0.0	0.0	0.0
Tricoptera								
Arctopsyche sp.	1.4	0.6	1.3	0.4	6.2	2.4	0.9	3.2
Glossosoma sp.	0.1	0.1	0.2	0.0	1.3	0.05	0.0	10.7
Lepidostomatidae sp. 1	1.7	0.3	0.4	1.1	2.5	0.6	0.6	1.2
Lepidostomatidae sp. 2	0.4	0.0	1.2	0.05	0.1	0.8	0.0	0.0
Lepidostomatidae sp. 3	0.0	0.04	0.0	0.0	0.5	0.0	0.0	0.0
Limnephilidae sp. 1	0.7	0.0	0.8	0.05	0.2	0.5	0.0	2.0
Limnephilidae sp. 2	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Rhyacophila sp. 1	6.5	6.3	1.9	1.6	2.4	4.8	1.8	1.9
Rhyacophila sp. 2	1.2	2.2	2.0	1.6	4.0	3.6	4.2	2.5
Rhyacophila sp. 3	0.2	0.04	0.8	0.3	0.0	0.3	0.1	0.05
Rhyacophila sp. 4	0.2	0.1	0.0	0.0	1.6	1.2	0.1	0.8
Rhyacophila sp. 5	0.0	0.1	0.0	0.05	0.0	0.0	0.05	0.0
Rhyacophila sp. 6	0.0	0.0	0.0	0.5	0.0	0.0	0.05	0.0
Unident. Tricoptera sp. 1	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Unident. Tricoptera sp. 2	0.0	0.0	0.0	0.0	0.0	0.0	0.05	0.0
Unident. Tricoptera sp. 3	0.0	0.1	0.0	0.0	0.8	0.0	0.0	1.8
Diptera								
Bezzia sp.	1.0	0.2	0.5	5.2	5.6	5.5	10.1	10.4
Blepharoceridae sp. 1	0.2	0.0	0.4	0.0	0.7	0.2	0.0	1.4
Simulidae sp. 1	0.0	6.0	0.0	1.1	2.6	0.0	2.4	4.9
Simulidae sp. 2	0.0	0.0	0.1	0.05	0.0	0.0	0.0	0.0
Simulidae sp. 3	0.4	2.5	2.3	0.4	0.2	3.6	0.5	0.2
Tipulidae sp. 1	0.2	0.0	0.04	0.05	0.05	0.1	0.0	0.4
Tipulidae sp. 2	0.0	0.0	0.0	0.0	0.0	0.05	0.0	0.0
Tipulidae sp. 3	0.0	0.1	0.0	0.0	0.0	0.0	0.2	0.1
Tipulidae sp. 4	0.2	1.0	0.2	0.2	0.2	0.2	1.0	0.7
Tipulidae sp. 5	0.4	0.0	0.2	0.0	0.0	0.1	0.0	0.0
Unident. Diptera sp. 1	0.1	0.04	0.04	0.1	0.5	0.3	0.3	0.3
Unident. Diptera sp. 2	0.1	0.0	0.1	0.0	0.05	0.2	0.05	0.2
Unident. Diptera sp. 3	2.4	0.04	3.3	0.1	0.1	5.0	0.1	1.2
Unident. Diptera sp. 4	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0

TABLE 51. (Continued)

Species	1970		1972			1973		
Unident. Diptera sp. 5	0.0	0.0	0.0	0.05	0.0	0.05	0.0	0.0
Unident. Diptera sp. 6	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Unident. Diptera sp. 7	0.0	0.0	0.3	0.0	0.0	0.2	0.0	0.0
Unident. Diptera sp. 8	0.0	0.0	0.0	0.0	0.0	0.05	0.0	0.0
Unident. Diptera sp. 9	0.0	0.0	0.0	0.0	0.0	0.05	0.0	0.0
Coleoptera								
Cleptelmis sp.	1.2	1.6	2.6	0.4	11.6	1.4	6.4	0.8
Dytiscidae sp. 1	0.04	0.0	0.3	0.0	0.0	0.1	0.0	0.0
Dytiscidae sp. 2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.05
Heterlimnius sp.	0.9	3.2	1.6	4.2	5.6	1.9	4.1	15.4
Unident. Coleoptera sp.1	0.0	0.0	0.04	0.05	0.05	0.0	0.0	0.0
Miscellaneous								
Unident. Ephemeroptera spp.	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.1
Unident. Plecoptera spp.	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.2
Unident. Tricoptera spp.	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.2
TOTAL	74.8	173.1	151.2	169.4	206.6	212.1	193.3	248.0

TABLE 52. Median number of individuals per one-tenth square meter of the important trout food organisms in Nash Fork Creek for each sampling period in 1970, 1972, and 1973. Mean Values are in parentheses.

	May/June			July		August	
	1970	1972	1973	1970	1973	1972	1973
Ephemeroptera							
Baetis spp.	2.0(2.9)	10.0(40.9)	11.5(25.4)	75.0(84.6)	26.0(31.8)	24.5(25.2)	17.5(16.7)
Cinygmula sp.	15.0(20.3)	25.0(47.7)	67.0(73.5)	11.0(12.8)	17.0(21.4)	3.5(4.4)	8.0(9.2)
Epeorus longimanus	*	5.0(10.2)	19.0(22.0)	10.0(9.8)	10.5(14.2)	6.5(11.2)	2.0(6.4)
Ephemerella doddsi	1.0(3.0)	1.0(6.4)	1.5(11.4)	*	2.5(2.6)	17.5(29.0)	13.0(33.4)
Rithrogena brunnea	5.0(5.6)	4.0(8.3)	23.0(26.2)	4.0(7.0)	27.0(36.9)	33.0(45.1)	37.0(48.9)
Plecoptera							
Alloperla borealis	3.0(4.4)	2.0(5.9)	5.5(8.0)	3.0(5.8)	19.0(24.8)	7.0(9.5)	30.5(32.0)
Alloperla lineosa	**	**	**	1.0(2.2)	1.0(2.0)	*	*
Tricoptera							
Arctopsyche sp.	1.0(1.4)	1.0(1.3)	1.5(2.4)	*	*	4.0(6.2)	1.0(3.2)
Glossosoma sp.	*	*	*	*	*	1.0(1.3)	3.5(10.7)
Rhyacophila spp.	3.0(8.1)	3.0(4.7)	8.5(9.9)	5.0(8.7)	3.0(6.3)	5.0(8.0)	3.0(5.2)
Diptera							
Simulidae spp.	*	2.0(2.4)	0.0(3.6)	1.0(8.5)	1.0(2.9)	2.0(2.8)	0.0(5.1)
TOTAL	66.0(74.8)	114.0(151.2)	174.5(212.1)	164.0(173.1)	177.5(193.3)	156.0(206.6)	267(248.0)

*Mean value is <1.

**Individuals were too small to be positively identified as *A. lineosa*.

——Pairs are not significantly different at .05 level.

---Pairs are not significantly different at .01 level.

This difference in the initiation of the runoff between 1972 and 1973 can be used to explain the significant differences found between the 1972 and 1973 populations of these three species. It also accounts for the significant difference in the total number of organisms found in May for these two years, since 75% of the increase in total numbers from 1972 to 1973 was due to increases in the densities of these species.

However, the difference in total numbers of organisms in May between 1970 and 1973 is not related to any differences in the run-off pattern in these two years. The low numbers found in 1970 were most likely a result of the low numbers of Baetis spp. Approximately 95% of the individuals of this genus are Baetis bicaudatus, a very specialized species found in association with dense growths of the alga, Hydrurus sp. In 1972 60% of the Baetis spp. were found in the two samples taken from an area with Hydrurus while in 1973 45% were found in the only sample taken from this type of habitat. Since this habitat was not sampled in 1970, we can only conclude that the population density of Baetis spp., and Baetis bicaudatus in particular, was underestimated in 1970 due to random errors in sampling and the low frequency with which these habitat types are encountered.

Baetis bicaudatus emerges from mid to late July and is replaced by Baetis intermedius, a very widely distributed and abundant species (Table 53). The low numbers of the latter found in July, 1973, and the high numbers found in July, 1970, are difficult to interpret. Both years were characterized by peak flows in late June which coincides with the period of time when this species is most vulnerable to downstream displacement because of its small size at that time. Likewise, the large numbers of Allopera borealis in both July and August of 1973, Glossosoma sp. in August 1973, and Baetis tricaudatus in July 1970, are not related to any obvious physical or abiotic changes. That large fluctuations of species populations do occur has been documented by Maciolek and Needham (1951). Their estimates of the standing crop of aquatic invertebrates in Convict Creek, California, varied from 76 kg/ha to 221 kg/ha over a five year period.

TABLE 53. Mean number of individuals per one-tenth m^2 of the more common species found in North French Creek in 1972.

	July 6,10 (n = 13)	August 2 (n = 11)
Ephemeroptera		
Baetis bicaudatus	22.5	4.6
Baetis intermedius	0.0	33.9
Cinygmula sp.	46.8	20.8
Epeorus longimanus	13.3	9.0
Ephemerella doddsi	0.6	8.4
Ephemerella inermis	6.6	0.0
Rithrogena brunnea	4.1	5.5
Plecoptera		
Nemoura oregonensis	4.1	12.4
Diptera		
Simulidae spp.	1.2	21.1
Coleoptera		
Heteroliminus sp.	113.8	84.5
Total	248.8	243.1

The invertebrate populations were also censused in North French Creek in 1972 (Table 53). Although the species composition was essentially the same in both Nash Fork Creek and North French Creek, the abundance of most species was higher in the latter. The large numbers of Heterlimnius sp. found in North French Creek resulted in a higher total number of organisms (248.8 per one-tenth square meter) as compared to Nash Fork Creek (169.4 per one-tenth square meter) in mid-July. The difference, however, was not statistically significant using the Mann-Whitney test. The dense brook trout population found in North French Creek could be, in part, a result of these high invertebrate populations.

Estimates of the total winter precipitation (snow) and data on the shape and magnitude of the spring snowmelt runoff curves for Nash Fork Creek were obtained from WRRI for the winters of 1969-70, 1971-72, and 1972-73. This information together with the quantitative estimates of the invertebrate populations in Nash Fork Creek provided the information needed to evaluate the ecological impact of increased snowpack on the population densities of the important trout food organisms. The data on snow precipitation were from the Little Brooklyn Lake climatological station, located at 3170 m and 1.5 km upstream from the Nash Fork Creek streamflow gauge. Total snow precipitation was 18.2 cm in 1969-70, 17.8 cm in 1971-72, and 14.8 cm in 1972-73.

Changes in the volume flow of Nash Fork Creek as a result of spring snowmelt are shown in Fig. 40. Although the snowpack was essentially the same for 1970 and 1972, the runoff curves are decidedly different. An early runoff was characteristic of 1972 with the peak flow occurring almost three weeks before the peak flow was reached in 1970. The mean air temperature for the period from May 23 to June 16 was 8.5°C in 1972 and 4.8°C in 1970. The temperature data were collected at the Medicine Bow Ski Area Climatological Station, which is located at 2774 m and very close to Nash Fork Creek. The runoff curve for 1973 has two distinct peaks and was similar in this respect to the 1970 curve, although the early peak was less pronounced

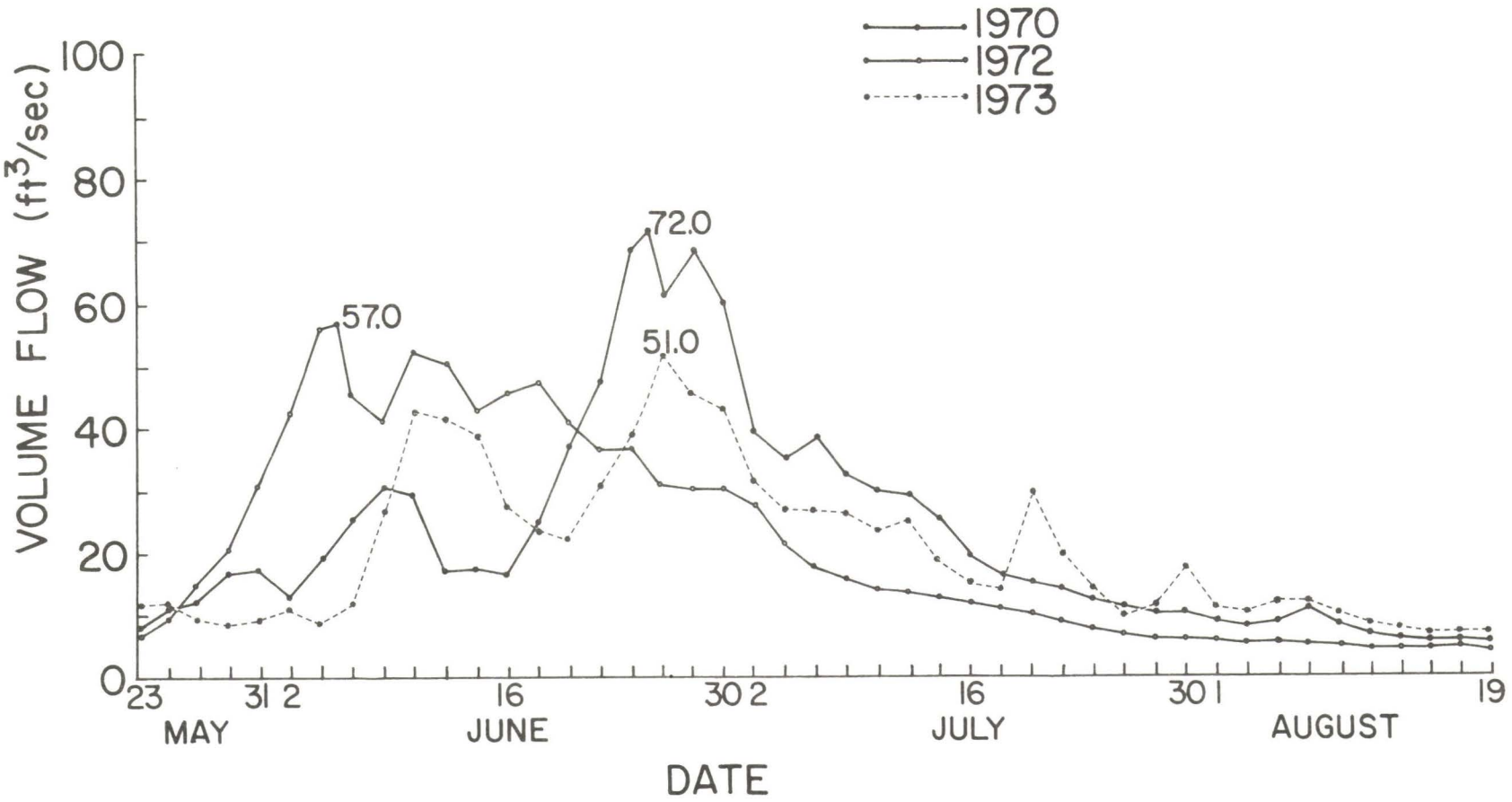

Fig. 40. Variation in the hydrographs of Nash Fork Creek during the summers of 1970, 1972, and 1973. The data were collected near Brooklyn Lodge, approximately 1 km upstream from the S. H. Knight Science Camp, by the Water Resources Research Institute.

in the latter. The sharp drop in the volume flow of Nash Fork Creek in mid-June of 1970 and 1973 coincided with the lower mean daily temperatures during the same period. Although 1973 was a year of low snowpack compared to 1970 and 1972, the difference in the peak flow values between 1972 and 1973 was less than the difference in the peak flow values between 1970 and 1972. Thus, air temperature in late spring rather than the depth of the snowpack in winter determined the date and magnitude of the peak flow as well as the general shape of the hydrograph shown in Fig. 40.

In summary, the density of aquatic invertebrate populations in those streams characterized by a period of increased flow due to spring snowmelt may vary widely during the runoff period. Some species such as Alloperla borealis and Rithrogena brunnea are emerging during the runoff while a few such as Epeorus longimanus and Baetis intermedius may be hatching. The majority of species, however, are subject to varying degrees of downstream displacement during the runoff. Factors such as the time and magnitude of the peak flow are important in determining the biomass of invertebrates. available to trout as food. These factors are dependent upon atmospheric conditions, in particular air temperature in May and June. If higher air temperatures occur in the spring and thereby prematurely initiate the melting of the snowpack, then lower population levels of many of the invertebrate species in Nash Fork Creek could result.

Relationships Between Fish Production and Runoff

Allen (1969) discussed the factors which limit the production of salmonids in streams and included the extent of spawning habitat, volume of stream discharge, permeability of gravel, predation, territoriality, density of population, and amount of food eaten. He noted also that "climatic factors, particularly temperature, may also exert a direct influence on growth and hence on production."

Spawning habitat in the Medicine Bow Mountains, including permeable gravels, is probably never in short supply for stream-dwelling trout nor to lake dwellers in the drainage lakes. In a few lakes, e.g. Mirror Lake, spawning habitat is inadequate and in other lakes (Silver Lake, Libby Lake) the brook trout are forced to migrate downstream into the outlets to spawn. If anything, the slow growth of brook trout in North French Creek suggests that spawning can sometimes be too successful, leading to overcrowding.

Excessive predation, including cannibalism, has not been observed in the Medicine Bow Mountains and is not believed to be important in restricting production. The other factors listed by Allen (1969) are of importance and will be considered here in relation to annual snowpack and volume of runoff.

Temperature

Water temperatures exert a dominating influence on the ecology of aquatic organisms. The different rates of growth of the brook trout in different habitats shown in (Table 47 and Fig. 19, page 233 and 89, respectively) are to some extent due to differences in water temperature but it is difficult to evaluate the significance of this compared with other influences such as population density and availability of food. Several aspects of this study focused upon the influence of temperature on growth.

In the analysis of the growth of brook trout of all ages and especially those from Nash Fork Creek at the Science Camp, the annual increment of growth in different calendar years was estimated by back-calculation using annual marks on the scales. These estimates did not suggest any real differences and were generally unsatisfactory. In spite of several special precautions taken to attempt to refine the back-calculation of length-at-age (see Methods, p. 228), it is not believed at this time that this technique is sufficiently sensitive to detect the year-to-year differences in growth which might result from the differences in climatic factors which occurred in the period 1970 through 1973.

TABLE 54. Growth of Age 0 Brook trout in water of different mean temperature.

Habitat	Libby Cr.	N. French	Telephone Cr.	Sci. Camp	Ski Area
Elevation (m)	3300	3000	3200	3100	2700
Mean Water T (C)*	8.3	8.8	11.7	11.2	11.1
Wt. of Age 0 trout, Sept. 21, '74 (gm)	1.36	1.67	2.41	2.73	2.50

Underlined values not significantly different at .05 level.

* From 30 measurements taken between June 26 and Sept. 21, 1974.

Another analysis was the empirical measurement of growth of Age 0 brook trout in different habitats. Preliminary data collected in 1972 and 1973 were promising and in 1974 growth and water temperatures were measured at five stream localities. A general correlation between growth and water temperature is indicated, Table 54. It is interesting to note that water temperatures were higher in Telephone Creek but that growth of the Age 0 trout was slower. This is probably explained by the observation that insolation of the stream waters in the open at 3200 m is greater and so water temperatures during the months of June, July and August are higher than downstream where the stream is torrential and heavily shaded. An explanation for the slower growth of the Age 0 trout in Telephone Creek is that lower temperatures prevail in May and early June when the spring runoff is delayed by about two weeks at higher elevations. We do not have water temperatures for that period but the trend is shown even in late June when in 1974 daily water temperatures in Telephone Creek were lower than those at Science Camp until July 5, after which they were consistently higher in Telephone Creek until September 21.

Water temperature data for Nash Fork Creek at 3000 m elevation were recorded by Good (1974) and during this study. Data or volume flow, snowpack, and air temperature are available from the records compiled by the Soil Conservation Service and by WRRI (Allen and Smith 1972, Rechard and Smith 1972). Some relationships between water temperature, air temperature, snow depth in the drainage area, and volume flow are shown in Table 55 and Fig. 41. The negative correlation between water temperature and spring's streamflow volume, together with that between water temperature and trout growth (Table 54) support the conclusion that, generally, increased snowpack at this elevation lowers spring water temperatures, shortens the growing season, and slows the growth of brook trout. On the other hand, in torrential streams with reduced flows after the main part of the runoff, water temperatures are also strongly influenced by insolation. The highest mean daily water temperatures were recorded in 1972 and 1973 when maximum air temperatures were also recorded.

TABLE 55. Snowpack, air and water temperature relationships in the Nash Fork drainage.

Year	1969	1970	1971	1972	1973	1974
Snow depth (cm)	20.9	35.4	41.3	29.5	27.6	30.3
Water content (cm)	6.73	13.6	16.5	11.5	9.6	12.2
May-Aug. volume flow (ha.-m.)**	342	525	569	495	472	552
Maximum mean Water T	12.2	12.5	12.5	14.9	14.4	13.3
Mean Water T July 1-5	11.1	9.4	7.8	11.1	11.5	10.4
Mean Water T Aug. 1-15	11.3	10.8	10.9	13.3	11.9	10.3
Mean Air T May-June	3.6	*	4.2	5.8	2.8	3.3
Mean Air T July-Aug	11.4	11.1	10.8	11.1	11.1	10.0
First date of Max. Mean T.	7/1	7/8	7/16	7/18	7/11	7/13
First date of 10 C mean water T.	before 7/1	7/4	7/13	6/28	by 6/28	6/24

* missing data
**ha.-m. equals the amount of water required to cover one hectare one meter deep, or 10,000 m^3.

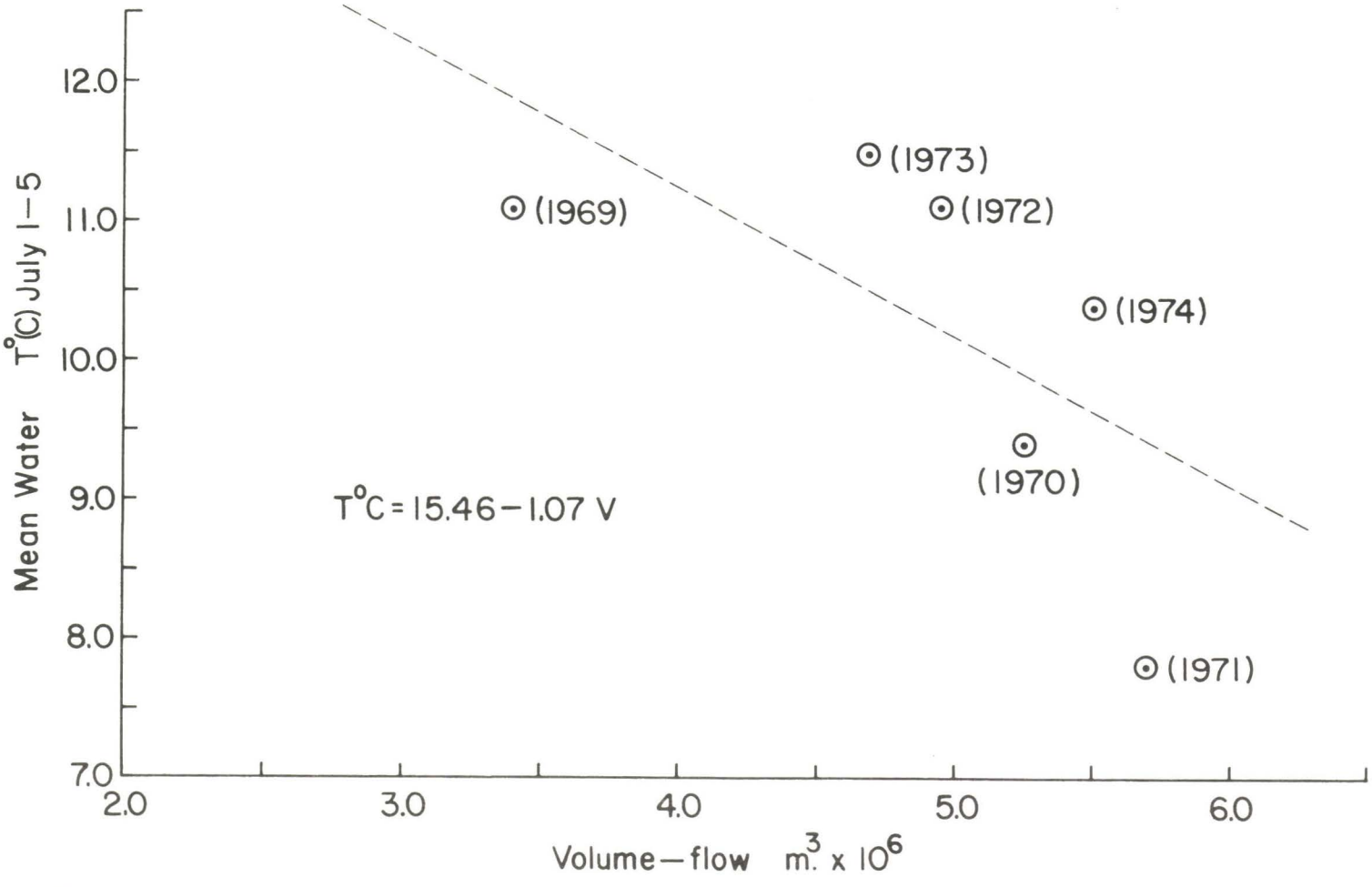

Fig. 41. Mean water temperature in relation to volume flow for Nash Fork Creek during the period July 1 - 5.

Stream water temperatures are apparently related to volume flow and snowpack before about mid-July but probably more to air temperatures after that date.

Availability of Food and Population Density

No clearcut correlations were shown in this study between growth of trout, population densities, and available food. In North French Creek, where growth was slowest and densities are higher, food is at least as plentiful as in streams where growth occurs more rapidly (Table 53). Mean temperature is lower than in Nash Fork Creek, however. It is not possible with the data at hand to calculate correlations between growth, population densities, available food and water temperatures. Such an analysis would require the type of data we have for Nash Fork Creek alone from several stream fisheries in the Snowy Range area and for several years, ideally collected during years of contrasting climatic conditions. Such data are currently not available.

Predicted Effects of Increased Snowpack on Trout Production

The snowpack and volume runoff were very similar in the years 1972, 1973 and 1974 (Table 55), and therefore no opportunity was provided during the course of this study to correlate fish production and runoff directly. Attempts to measure differences in growth in the light snowpack year 1969 by back-calculation were inconclusive. From our demonstration of slower growth of Age 0 fish in streams of lower water temperature, and from the negative correlation shown to exist between snowpack and water temperatures, it may be inferred that increased snowpack would decrease trout growth at least during the early part of the growing season.

In this study the biomass of stream invertebrates was not affected significantly by differences in total volume of runoff. Apparently increased snowpack would not adversely affect the availability of trout food. At present we have no factual basis for judging whether or not increased volume flow might affect the density of trout populations, and thereby effect a change in trout production. The differences in stock density between Nash Fork Creek and North French Creek are apparently related to better spawning facilities. We believe that the

slower growth of brook trout in North French Creek is probably related to both higher population densities and lower average water temperatures.

It would appear that a moderate increase in snowpack in the Snowy Range area would not affect trout production to any great extent. If it had any effect, it would apparently be to decrease production. Barring very drastic increases in snowpack and volume of spring runoff, the production of trout and benthic invertebrates are apparently influenced as much by variations in the pattern of runoff and by late summer air temperatures as they are by the volume of snowpack and runoff.

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THE EFFECT OF SPRING RUNOFF ON SUBALPINE LAKE PHYTOPLANKTON

M. Parker and S. H. Condit

Several studies have considered the effects of runoff on lakes (Brook and Woodward 1956; Kalff 1967B; Efford 1967; Olsen, Chakravarti and Olson 1967; Welch, Buckle, and Bush 1972; Nicola and Borgenson 1970). Olsen et al. (1967) found that high winter flushing caused low nutrient levels in the spring. Diluting nutrients to levels that prevent algal blooms by increasing the flushing rate of a lake is one method of controlling eutrophication (Welch et al. 1972), though runoff waters can also add nutrients to a lake (Gearheart 1973). Both the increase of nutrients in a lake and the dilution of nutrients in a lake are mentioned by Findenegg (1965), who says that an increase is likely to occur if the lake receives its influent from an upstream lake. Nicola et al. (1970) noted that the turbidity in a lake increased during runoff. Kalff (1967b) found that runoff warmed an arctic lake, while Efford (1967) found that heavy spring runoff delayed the warming of a Canadian lake. Brook et al. (1956) studied the effect of runoff on the flushing rate or retention time of a lake, and found that if the retention time is less than ten days (i.e. if the flushing rate is greater than 0.1 gC/gC/day) a significant phytoplankton standing crop could not develop.

Brooking (1972) found that neither turbidity nor nutrient levels changed significantly during runoff in Nash Fork Creek in the Medicine Bow Mountains, results that can be generalized to Libby Creek (Skinner, personal communication). Skinner (personal communication) feels that runoff has no significant effect on the nutrient levels in Libby Lake.

There are no nutrient data available for Libby Lake, however, or for the lake above from which Libby Lake receives the major portion of its inflow.

Of the possible effects of runoff mentioned in the literature, changes in water temperature and changes in the flushing rate are probably of greatest importance for montane lakes in the Medicine Bow Mountains. Thus, using modeling techniques and data from Libby Lake, we proceeded to test the following 2 hypotheses in the limited time available.

1) During spring the volume flow of runoff is above a "critical" level, flushing losses of the phytoplankton exceed photosynthetic gains, and the algal population decreases.
2) If the above is true, weather modification will increase the volume flow of runoff, and hence decrease the algal standing crop to levels lower than would otherwise occur.[1]

Study Area

Libby Lake is an oligotrophic lake with a surface area of 103 hectares, an average depth of 4.8 m, and a maximum depth of 12.5 m (Sinn 1961, Fig. 42). The bottom consists of boulders and boulders covered with muck. The lake is at an elevation of 3277 m (Sinn 1961), is ice covered from October or November to late June, and stratifies weakly during the summer. Libby Lake is the last in a chain of 4 glacial lakes and several ponds. Its major inlet is from the lake above, but snowmelt runoff from adjacent land also contributes to the inflow. The only outlet is Libby Creek, which flows all year.

Wind is an important factor in the Libby Lake ecosystem. During the period 1966 to 1969 the average daily wind speed from June to September was 22 kph at a station approximately 0.7 km from Libby Lake (Smith 1970, Rechard and Smith 1972).

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[1] Non-scientists may wish to turn to page 321 for the conclusions.

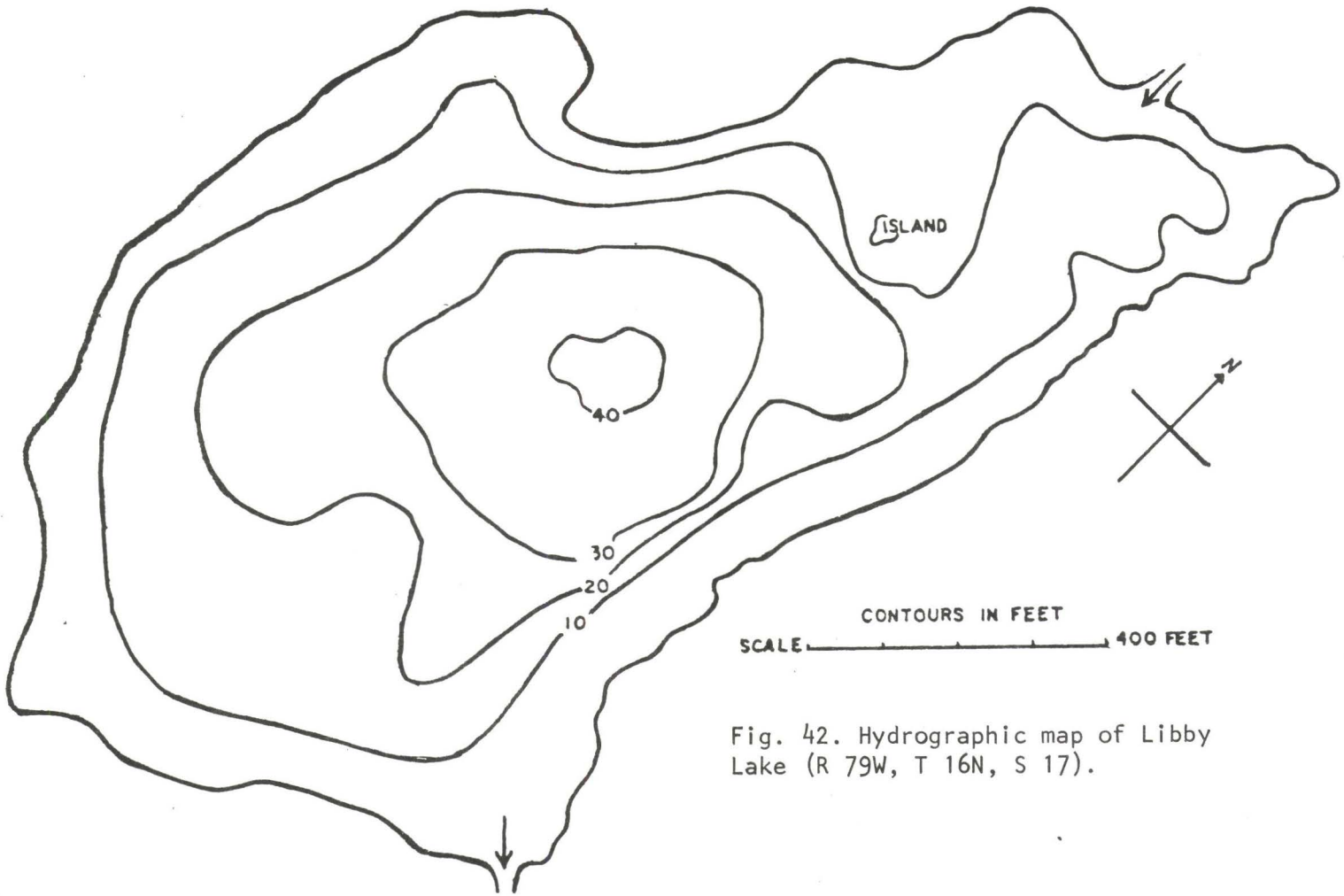

Fig. 42. Hydrographic map of Libby Lake (R 79W, T 16N, S 17).

Methods

Dissolved oxygen and alkalinity (phenolphthalein, methyl orange) were measured according to methods in American Public Health Association (1971), pH was measured with a Beckman pH meter, temperature profiles were taken with a Whitney underwater thermometer, and light was measured with a G.M. submarine photometer.

Phytoplankton samples were collected with a water bottle, preserved with Lugol's solution, and concentrated by aspiration after settling. Enumerations were made using an inverted microscope with a 40x objective. Samples for chlorophyll analyses were also collected with a water bottle. The extraction method and equations of Strickland and Parsons (1968) were then used to calculate the mg chlorophyll a m^{-3}.

Zooplankton were collected with a Clarke-Bumpus sampler and preserved with 10 percent formalin. Enumerations were made using a Sedgewick-Rafter cell and dissecting microscope.

Primary production was measured in the field using the methods outlined by Saunders et al. (1962) and Vollenweider (1965, 1969). Data on mg C m^{-3} incubation^{-1} were converted to daily rates as described by Vollenweider (1965). Primary production was estimated on IV-22-74 and IV-29-74 as follows. The phytoplankton standing crop (mg chl *a* m^{-3}) at each sampling depth was multiplied by (mg C mg chl *a*$^{-1}$ hr incubation) obtained from the ^{14}C experiment of V-5-74. These data of mg C m^{-3} hr incubation^{-1} were then plotted versus depth.

I'_k is a measure of phytoplankton adaptation to different light and temperature regimes (Vollenweider 1965). In the model XKP is equivalent to I'_k. In order to calculate XKP, the data from each ^{14}C experiment were plotted as mg C mg chl *a*$^{-1}$ day^{-1} versus light. The light intensity giving the maximum specific production rate in the absence of light inhibition was estimated from the graph (e.g. see Fig. 7 in Rodhe 1965). The light intensity thus obtained divided by available incoming radiation gave XKP as a fraction of incoming radiation for each experiment.

PMAX is the maximum observed specific production rate for any ^{14}C experiment. It was obtained by inspection from the data of each ^{14}C experiment graphed as mg C m^{-3} day^{-1} versus depth, and as mg C mg chl *a* $^{-1}$ day^{-1} versus light.

The Model

A program to calculate the daily change in the phytoplankton standing crop was written in the Flag version of the Fortran IV programming language to run on a Sigma 7, 8401 computer. The variable physical parameters in the model are light, temperature, and volume flow of runoff. All calculations were made with a time scale of one day. Output was usually obtained at 15 day intervals. Specific gross productivity is expressed as grams carbon assimilated per gram carbon of phytoplankton per day (gC/gC/day) and absolute gross productivity as grams carbon assimilated per cubic meter per day (gC/m^3/day).

The difference equation used to calculate the change in phytoplankton biomass per day was:

$$SC_{t+1}-SC_t = PSYN-SC_t\ [(RP)\ (Q_{10})+F+S]\ -G \qquad (1)$$

SC: average standing crop of phytoplankton on day t, gC/m^3

PSYN: total daily photosynthesis, gC/m^3/day (see equation 2)

RP: respiration loss at 15°C, gC/gC/day (see equation 6)

Q_{10}: modifies respiration losses according to temperature, unitless (see equation 7)

F: flushing loss, gC/gC/day (see equation 8)

S: sinking loss, gC/gC/day (see equation 9)

G: grazing loss to zooplankton, gC/m^3/day (see equation 10)

Possible losses not represented in the equation are excretion and parasitism. There is very little information on the amount and

effects of parasitism and it was not considered in this study. Excretion is discussed below.

Photosynthesis in gC/m^3/day was calculated from Vollenweider's (1969) modification of Talling's (1957b) equation (see also Talling 1957a; Vollenweider 1965; Fee 1969, 1973):

$$PSYN = \left(\frac{(SC)(0.8)(\lambda)(PMAX)}{K_w + K_p}\right)[\ln(1.48)(XLI/XKP)]\ )/4.8 \quad (2)$$

PSYN: total daily photosynthesis, gC/m^3/day

SC: average standing crop of phytoplankton on day t, gC/m^3

λ: daylength factor, hours/day (sunrise to sunset, from Percy 1972, p. 13-18)

PMAX: rate of photosynthesis at optimum light, gC/gC/hr (see equation 3)

XLI: photosynthetically usable light immediately below water surface, langleys/day (see equation 4)

XKP: measure of the light-temperature adaptation of the phytoplankton population, langleys/day

K_w: extinction coefficient of light by water, m^{-1}

K_p: extinction coefficient of light by phytoplankton, m^{-1}

0.8: constant to account for portion of day that light is not sufficient for photosynthesis to occur, unitless

1.48: constant regarding light, unitless

4.8: average depth of lake, m

ln: natural logarithm

PMAX, the maximum specific production rate in gC/gC/day, was varied with temperature according to a modification of Megard's (1972) equation:

$$PMAX = (0.0268)(TEMP) + 0.075 \quad (3)$$

TEMP: water temperature in °C, based on data from Libby Lake (see Fig. 44)

Megard presented PMAX as the maximum specific rate of photosynthesis in mgC/mg chlorophyll/day. This equation was converted to mgC/mgC/hr

using a conversion factor of 60mg C/mg chlorophyll (Strickland 1960). The constant 0.075 was lowered from Megard's value of 0.285 to obtain reasonable production rates for an oligotrophic lake.

XLI, the photosynthetically usable light immediately below the surface of the water in langleys/day, was calculated as:

$$XLI = 170 + (85)\ [\text{cosine}\ (TIME-176)/(365)(6.28312)] \quad (4)$$

TIME: day of year (1 to 365)

170,85,176,365,6.28312: constants used to fit data on light.

This function generates values that fit solar radiation data from the Medicine Bow Mountains (Smith 1973, pp. 50-61; Rechard and Smith 1972, pp. 93-4).

XKP, a measure of the light-temperature adaptation of the algae in langleys/day, varies seasonally (Ichimura 1960). XKP apparently is a function of light, temperature and nutrient concentration. However, these relationships are not well understood (Ichimura, Saijo and Aruga 1962; Ichimura 1960). The values of XKP used in the model were determined from data of Rodhe (1965), and met the criteria of keeping the quantity $\ln(1.48)(XLI/XKP)$ in the range of 2 to 3.5 (Vollenweider 1969). In the model XKP is expressed as a percentage of the total photosynthetically available light and is set at 0.05 during winter, 0.07 during spring and fall, and 0.09 during summer.

K_w, the extinction coefficient of water m^{-1}, was determined empirically from measurements in Libby Lake and was set at 0.45 m^{-1} in the model.

K_p, the extinction coefficient of light by phytoplankton (m^{-1}), was calculated by Talling's (1970) equation after conversion from extinction units/mg chlorophyll _a_ to extinction units/mg C. A conversion factor of 30 mgC/mg chlorophyll _a_ was used (Strickland 1960).

$$K_p = (SC)(0.333) \quad (5)$$

Respiration

The results of a literature search for values for phytoplankton respiration rates are summarized in Condit (1974). Respiration is a complex process and varies with temperature and possibly with light. Photorespiration, the process of oxygen uptake in the light, may be as high as twenty times the rate of dark respiration (Lex, Silvester and Stewart 1972). This process can lead to errors in both oxygen and 14-C productivity methods (Lex et al. 1972). Bunt (1965) decided that the respiration rates given by Steemann Nielsen and Hansen (1959a) were far too low, although he listed rates in the same range. Bunt concluded that light inhibits dark respiration and stimulates photorespiration, and that the process of respiration was not well enough understood to obtain accurate values for gross photosynthesis.

Steemann Nielsen et al. (1959a), whose values for respiration were used in the model, derived rates of respiration from 14-C data by graphing the photosynthesis-light curve and extrapolating the curve until it intersected the ordinate. The y intercept was then considered to be the rate of respiration. Other workers have said that the standard 14-C light and dark bottle method cannot be used to measure respiration (Ichimura and Saijo 1958), but the graphical technique of Steemann Nielsen et al. did not involve the use of dark bottles.

The respiration rate used in the model was 15 percent of the total carbon fixed at 15°C (RP is 0.15 at 15°C). Respiration losses were varied with temperature.

$$\text{respiration losses (gC/gC/day)} = (RP)(Q_{10}) \tag{6}$$

$$Q_{10} = 0.44 + (0.025)(TEMP)^2 \tag{7}$$

Flushing

Flushing rate in gC/gC/day was calculated by the equation

$$F = \frac{\text{volume of outflow}}{\text{volume of the lake}} \tag{8}$$

which is the inverse of the replacement coefficient (Brook and Woodward 1956). Data on runoff were obtained from the University of Wyoming

Water Resources Research Institute (hereafter termed WRRI: Rechard and Smith 1972; Allen and Smith 1972, 1973). Unfortunately the only data for the outflow of Libby Lake are from June 29, 1972 to September 30, 1972 (Allen and Smith 1973, p. 20). However, data for a complete year were generated by performing a linear regression on data from this station and a station further down Libby Creek. Estimates of winter volume flow in April 1974 agree with the volume flow estimated by linear regression. The volume flow versus time curve resulting from the linear regression was fitted by a series of equations, and these were used when manipulating flushing rates in the model.

WRRI data were consulted to determine what was reasonable variation for the time of occurrence of runoff, the magnitude of runoff and the shape of the runoff vs time curve. There appears to be relatively little variation in the time of occurrence of runoff in the Snowy Range (Fig. 43). Data on Libby Creek are available from 1968 to 1973, and the day of peak runoff varied from May 28 to June 35 (Allen and Smith 1972, 1973 data unpublished). The peak occurred on June 5 in 1972, and these data were used as the comparison year in the model simulations when the time of runoff was changed.

Data on the time of occurrence of runoff from Nash Fork Creek in the Snowy Range are similar to the data from Libby Creek. From 1967 to 1972 the day of peak runoff varied from June 26 to May 27 (Allen and Smith 1972, 1973). Runoff usually starts in mid-May and returns to non-flooding volume flows in September or October (Rechard and Smith 1972).

There are only four years of streamflow data for the Libby Creek Drainage (Rechard and Smith 1972, p. 116; U. S. Geological Survey 1968, 1969, 1970, 1971). It was found that the total volume flow of runoff in the Libby Creek Drainage for 1972 was 30 percent lower than a 55 year mean estimated for the Libby Creek Drainage. The estimated 55 year mean volume flow was used as the comparison year for determining the possible effects of changing the magnitude of runoff. 1972 was used as the comparison year when other runoff parameters were changed.

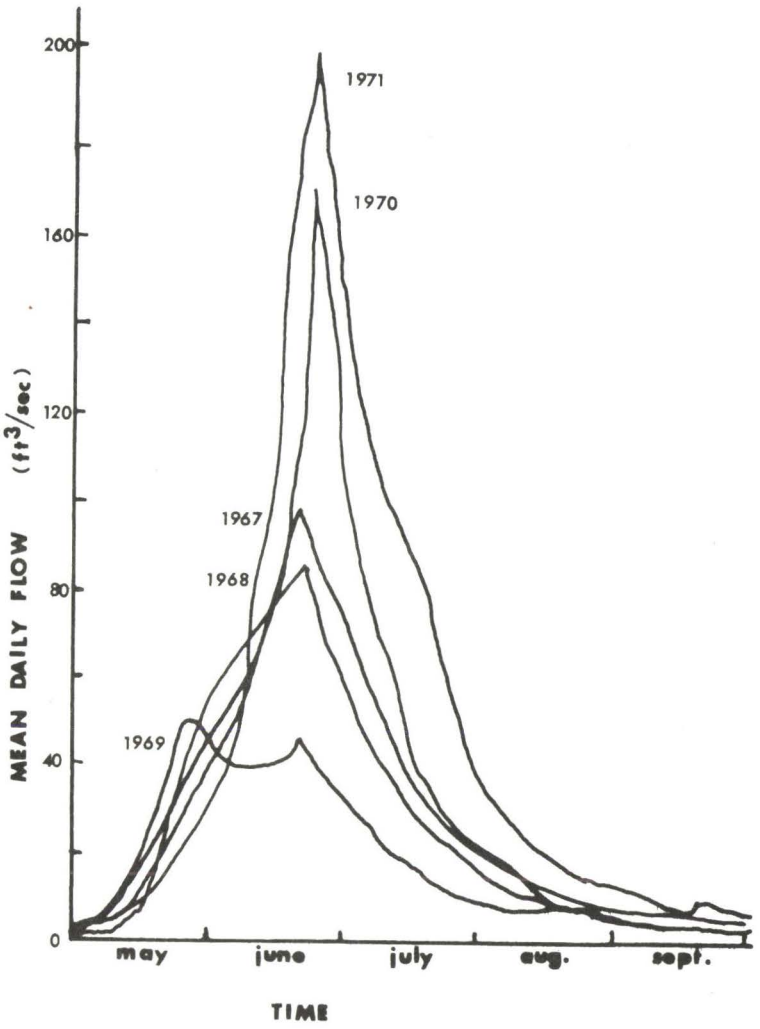

Fig. 43. Smoothed hydrographs for Nash Fork Creek, 1967 to 1971.

WRRI data suggest that the total volume flow of runoff in Libby Creek varies from year to year by plus or minus 30 percent (Rechard and Smith 1972, p. 100). The 1972 volume flow was 19 percent lower than the 4 year mean for Libby Creek for the period 1968 to 1971 (Rechard and Smith 1972). WRRI data also suggest that the maximum variation in total volume flow of runoff in the Snowy Range is approximately plus or minus 50 percent (Rechard and Smith 1972, p. 99). Changes in the shape of the runoff versus time curve were investigated because WRRI data suggested that changes in total volume flow of runoff are accompanied by changes in the shape of the runoff versus time curve (Fig. 43). The rising portion of the curve remains fairly constant, but the curve falls off faster in years of low runoff.

A major problem with calculating flushing rate by equation 8 is the possibility of short circuiting, which occurs when some portions of a basin flush more rapidly than others. Watters, Mangelson and George (1973) in their work on sewage ponds found that short circuiting is likely to occur if the inlet is directly in line with the outlet, and this is the case in Libby Lake (Fig. 42). Short circuiting is affected by wind and is especially likely to occur if the prevailing winds blow from the inlet toward the outlet. The opposite is true in Libby Lake where the prevailing winds blow from the southwest, or in general from the outlet toward the inlet (Fig. 42). It is not known if short circuiting occurs in Libby Lake, or the degree to which the wind might counteract it.

Sinking

Smayda (1970) comprehensively reviewed data on the sinking of phytoplankton on the sea. He found a range of sinking rates from 0.02 to 6150 m/day for cultured or natural populations of single cells, cell fragments, and large colonies. Of the total of 77 reported rates for the three categories, 11 are greater than 100 m/day, 10 are between 10 and 100 m/day, 8 are between 5 and 10 m/day, and 25 are less than 1 m/day. About 75 percent of all the rates reported by Smayda are less than 1 m/day. Since seawater is more dense than freshwater, the

sinking rates would be somewhat higher for freshwater algae similar to the marine algae reported on by Smayda. The apparent sinking rate in Libby Lake is likely to be lower than the absoluate sinking rate in still water because the upper waters of the lake are constantly mixed by the wind (at times the wind is so strong it is impossible to row a boat away from the shore). The sinking loss for the phytoplankton in the model is calculated as:

$$S\ (gC/gC/day) = SP/ZE \tag{9}$$

SP: apparent sinking rate in m/day

ZE: depth of the eplimnion, set at 12 m, changed to 9 m during summer stratification.

Grazing

The effects of zooplanktonic grazing on phytoplankton were investigated in a preliminary way. Grazing losses were calculated as

$$G\ (gC/m^3/day) = \left[\frac{SCZ(UH)(SC)(Q_{10})}{SC + XKH}\right]/4.8 \tag{10}$$

SCZ: average biomass of zooplankton on day t, gC/m^2

SC: average biomass of phytoplankton on day t, gC/m^3

UH: maximum ingestion rate of zooplankton, gC/gC/day

XKH: phytoplankton biomass level necessary to allow reasonable ingestion rates, gC/m^3

Q_{10}: see equation 7

4.8: average depth of lake, m

The difference equation used to calculate the change in zooplankton standing crop per day was:

$$SCZ_{t+1} - SCZ_t = (EH)(G) - (SCZ_t)\ [(RH+XMH)(Q_{10}) + (0.5)(F)] - ZDDM \tag{11}$$

SCZ: average biomass of zooplankton on day t, gC/m^2

EH: excretion losses, gC/gC/day, set at 0.5

G: grazing, gC/m^2/day (i.e. equation 10 multiplied by 4.8 m)

RH: respiration losses, gC/gC/day, set at .05 at 15°C

XMH: natural mortality, gC/gC/day, set at 0.05 at 15°C

Q_{10}: modifies losses according to temperature, unitless (see equation 7)

ZDDM: density dependent mortality factor, $gC/m^2/day$ (see equation 12)

F: flushing loss, gC/gC/day (see equation 8)

0.5: factor to account for resistance of zooplankton to flushing (i.e. swimming against current)

The density dependent mortality factor was calculated as:

$$ZDDM = \frac{(SCZ)(1.0)}{SCZ+0.95} \qquad (12)$$

These equations and parameter estimates are presented to aid the reader and havenot been justified empirically or from the literature. The parameters were judged suitable for present purposes since they provided reasonable grazing losses to the phytoplankton.

Excretion

Excretion rates reported in the literature ranged from 0.5 (Eppley and Sloan 1965) to 95 percent of 14-C assimilated (Fogg and Nalewajko 1964). Excretion rates are known to vary with time, light, species of algae, age of culture or population, physiological condition of algal cells, carbon dioxide concentration, oxygen concentration, and population density (Fogg 1971).

It has been stated that the 14-C productivity method measures gross productivity minus excretion losses (Fogg, Nalewajko and Watt 1965; Antia, McAllister, Parson, Stephens and Strickland 1963). If this is indeed the case, matching specific gross productivity output from the model to productivity data from 14-C studies should correct for excretory losses.

Excretion is a complex process which is affected by many factors whose interactions are not well understood. Because so little is known about the factors thatcontrol excretion rates and how they

interact, because the values for excretion rates vary so widely, and because no measurements of excretion rates were made in Libby Lake, excretion losses were not included in the model. It was assumed that excretion had been corrected for in the values used for productivity since these were based on 14-C experiments.

Results

Characteristics of Libby Lake

The average temperature of the thermally homogeneous layer (epilimnion after ice off) was fairly similar in 1972, 1973 and 1974 (Fig. 44A). The approximate depth of the thermally homogeneous layer varied somewhat more between the same years (Fig. 44B).

The following information suggests that runoff will mix with and flush only the upper thermally homogeneous layer of the lake, that little short circuiting occurs, and that water temperature profiles can be used to give a good indication of the depth of the lake's flushing layer. The data on water temperature of the lake and of the major inlet show that the inlet water was the same temperature as the upper layers of the lake water. There was little difference in the water temperature or in chlorophyll *a* m^{-3} in the epilimnion between station I and station II during 1972 and 1973. Chlorophyll *a* profiles were vertically homogeneous in the upper layers of the lake (e.g. Fig. 15). Finally, drogues released in the lake at various depths in the epilimnion moved rapidly with the prevailing winds from the center of the lake toward the inlet (however, releases were not made until late July when runoff was not at very high levels).

Ice thickness was approximately 110 cm in April 1974, with about 10 to 40 cm of snow, or snow and slush over the ice. This ice and snow cover transmitted about 2 percent of the incident radiation (extinction coefficient of 2.8 m^{-1}, transmission of 6 percent m^{-1}; these are apparent values, since they include albedo).

Crustacean zooplankton reached much higher population densities than indicated by Sinn (1961). The two dominant crustacean zooplankton were *Daphnia pulex* and *Cyclops bicuspidatus thomasi*. Population

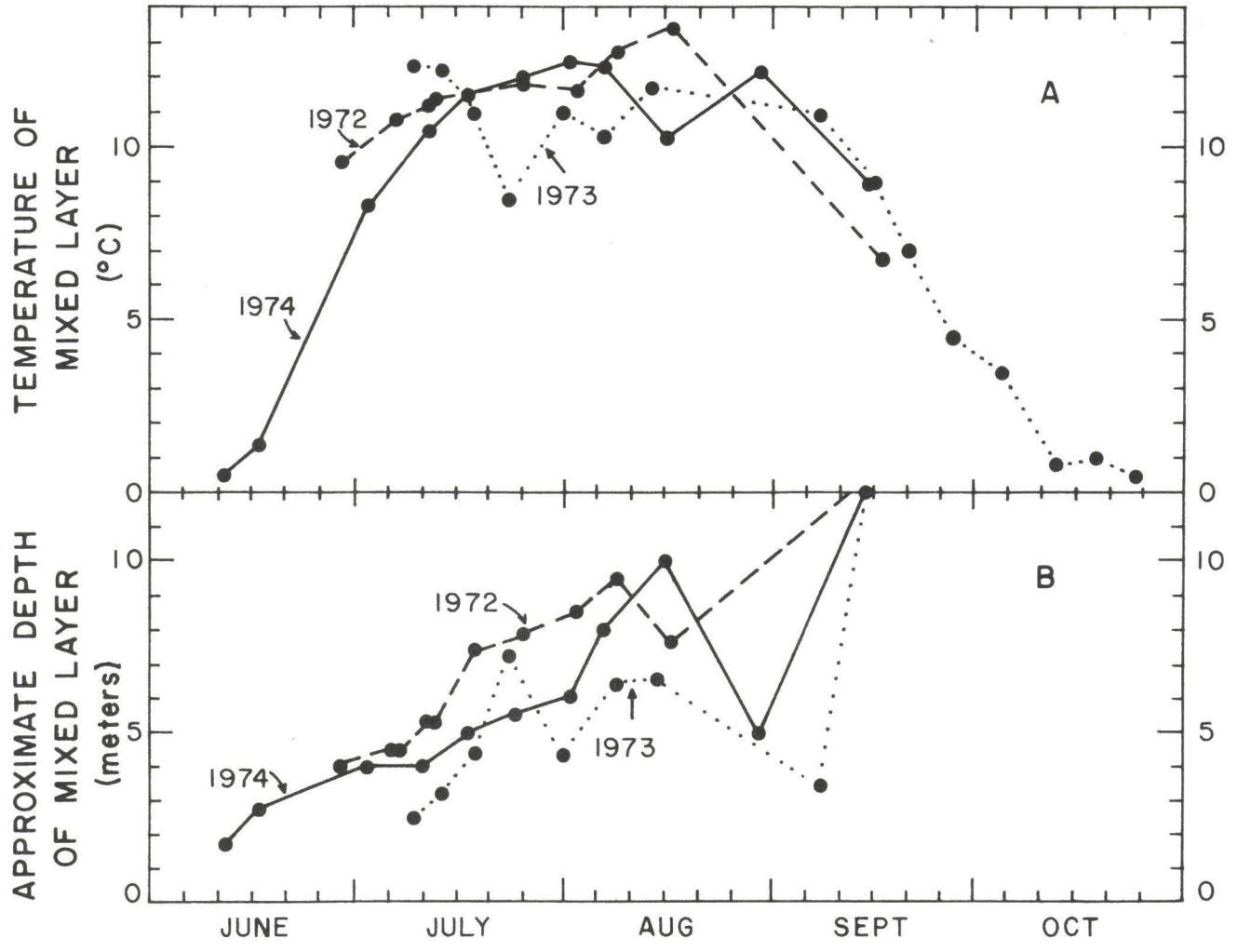

Fig. 44. A. Average temperature (°C) of the flushing layer (epilimnion) of Libby Lake in 1972, 1973, and 1974. B. Approximate depth of the flushing layer of Libby Lake in 1972, 1973, and 1974.

densities of these species in 1972 and 1973 are presented in Fig. 45. Fig. 45G presents the probable population size through time for D. pulex in 1974 based on initial semiquantitative analyses.

Although quantitative samples were taken in 1974 for phytoplankton enumeration, no counts have been made on the samples. The vertical distribution of algal biomass (mg chl a m^{-3}) is homogeneous with depth in the upper thermally homogeneous layer (Fig. 46). Considerably more biomass occurs in and below the thermocline. This pattern is similar to that found in previous years.

The average algal biomass m^{-3} peaked for 1974 under the ice before decreasing in late June owing to the effects of flushing (Fig. 47). The increase in July was due to a large biomass in the hypolimnion which was not affected by flushing. PMAX and XKP were reaching maximum values during this time, and absolute productivity also was greatest then (Fig. 50). The decrease in average algal biomass after mid-July corresponded with a period of increased runoff and a deepending of the epilimnion. After early August the hypolimnetic maxima of biomass was less than earlier. However, runoff and hence flushing was minimal, and the increasing biomass in the epilimnion led to an increasing average biomass.

A consideration of the algal biomass in only the flushing layer of the lake leads to a clearer understanding of the role of runoff and flushing. The depth of the flushing layer of the lake was determined by temperature profiles in conjunction with data on the temperature of the major inflow. After ice-off this flushing layer is the epilimnion. Algal biomass in the flushing layer is plotted with volume flow of Libby Creek versus time in Fig. 47.

Since the depth of the flushing layer varies with time, volume flow data alone do not accurately reflect the effect of flushing. The effect of flushing is directly related to retention time. Retention time was calculated as (volume of the flushing layer / average volume flow day^{-1} of the two days preceding the sample date). When data on retention time and the average algal biomass in the flushing layer are plotted versus time, it appears that the critical retention time

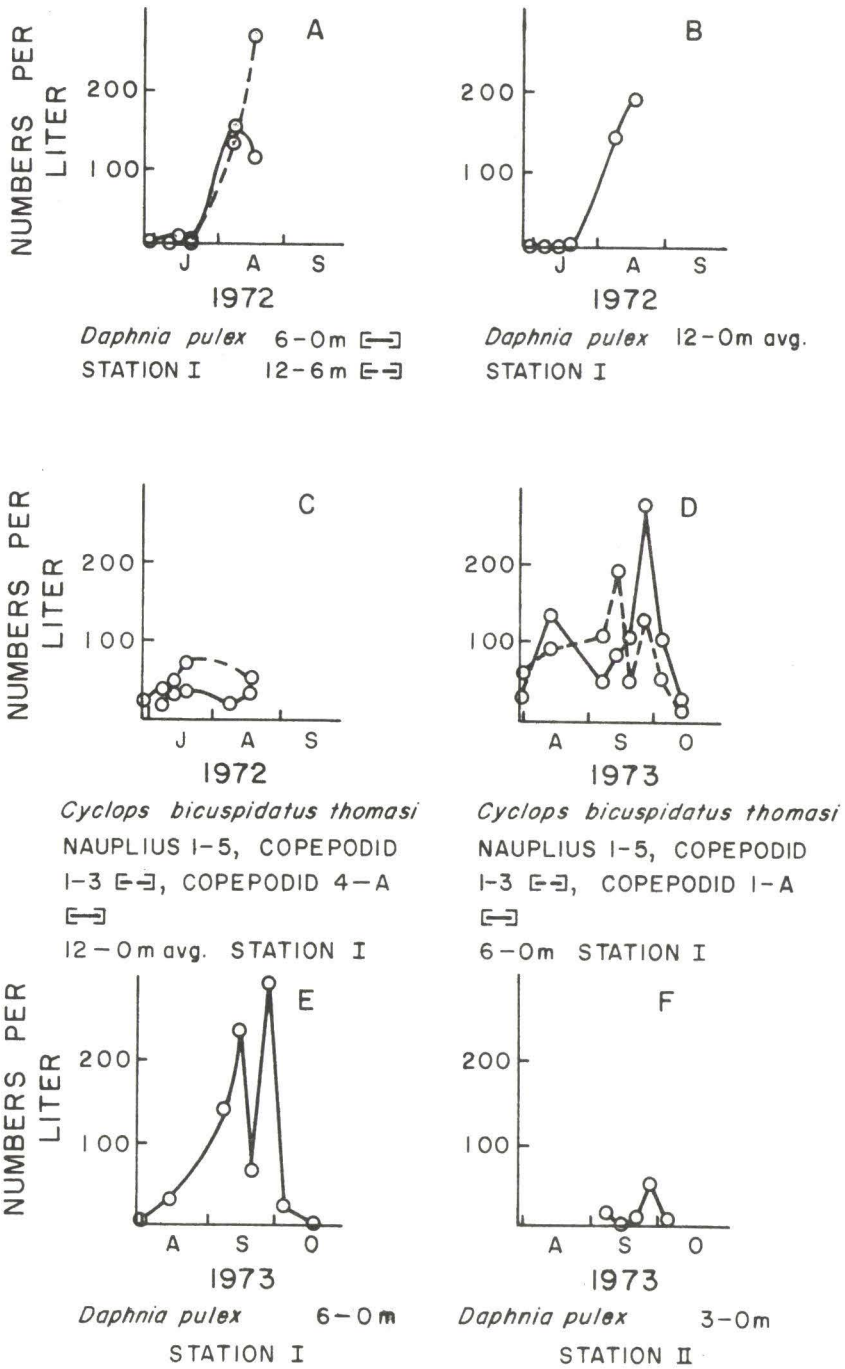

Fig. 45. A,B. Number/l of Daphnia pulex in Libby Lake (LL), Sta. 1, 1972. C. Number/l of Cyclops bicuspidatus thomasi in LL, Sta. 1, 1972. D. Number/l of C. bicuspidatus thomasi in LL, Sta. 1, 1973. E. Number/l of D. pulex in LL, Sta. 1, 1973. F. Number/l of D. pulex in LL, Sta. II, 1973. G. Probable relative numbers of D. pulex in LL, 1974, based on initial semi-quantitative observations.

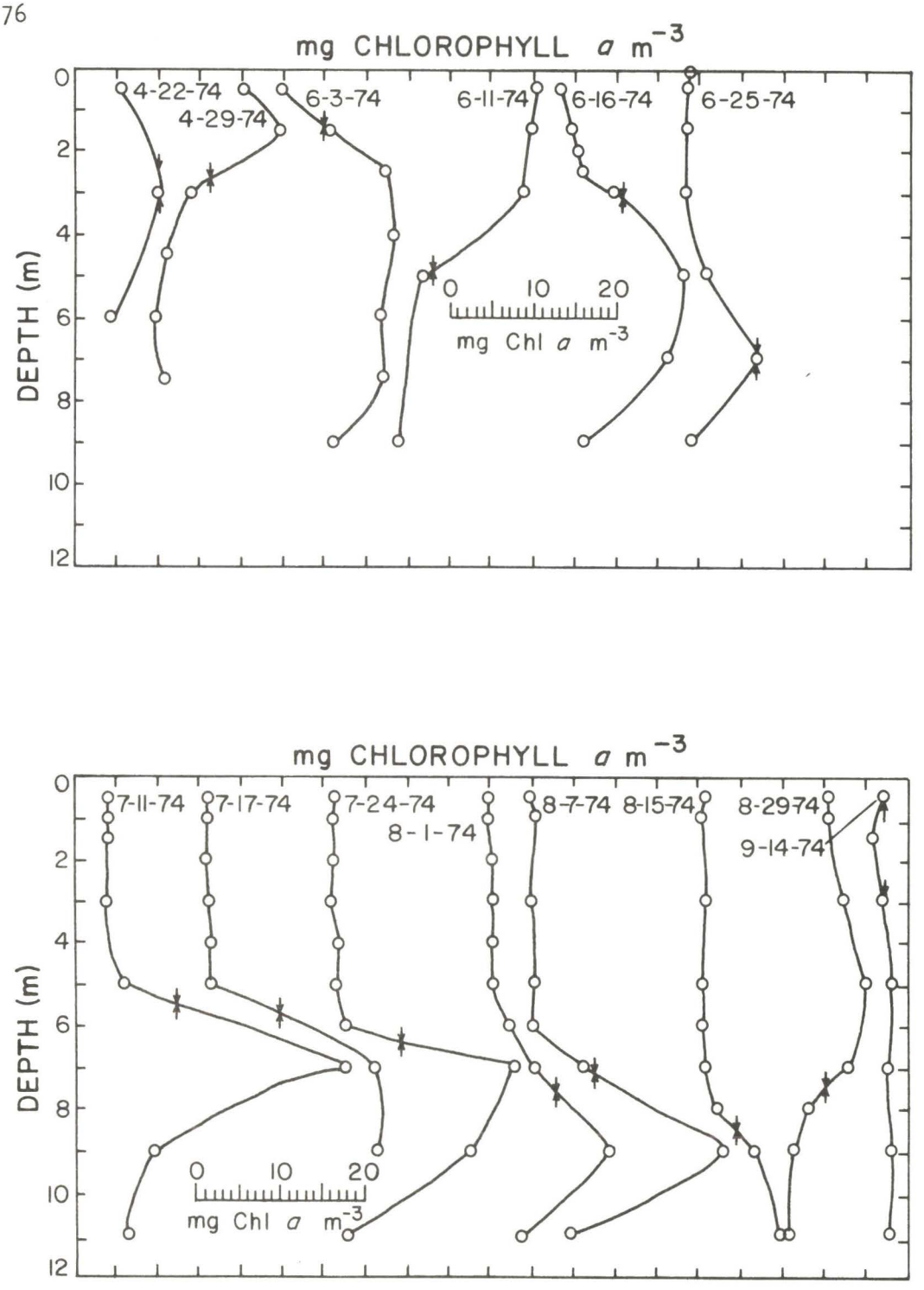

Fig. 46. Chlorophyll a m^{-3} versus depth in meters for 1974 sampling dates in Libby Lake. The arrows on each curve represent a value of 10 mg chl a m^{-3}. A scale of mg chl a m^{-3} is indicated on the graph. The lake was ice covered through the sampling date of June 16, 1974.

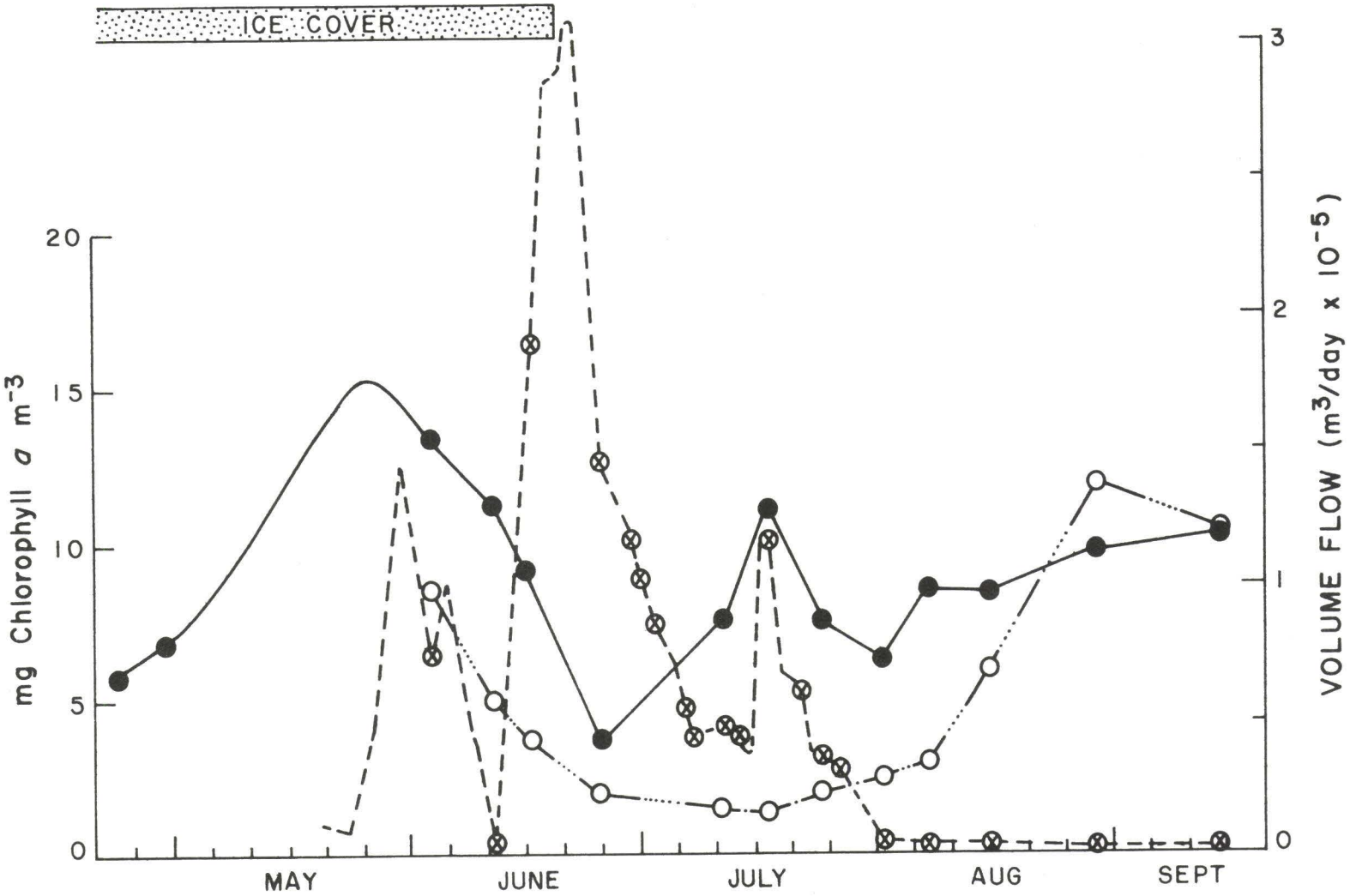

Fig. 47. Average chlorophyll a m^{-3} of the whole water column (solid line), of the flushing layer only (dot and dash line), and the volume flow in m^3 per day of Libby Creek just below Libby Lake (dashed line). All data are for 1974.

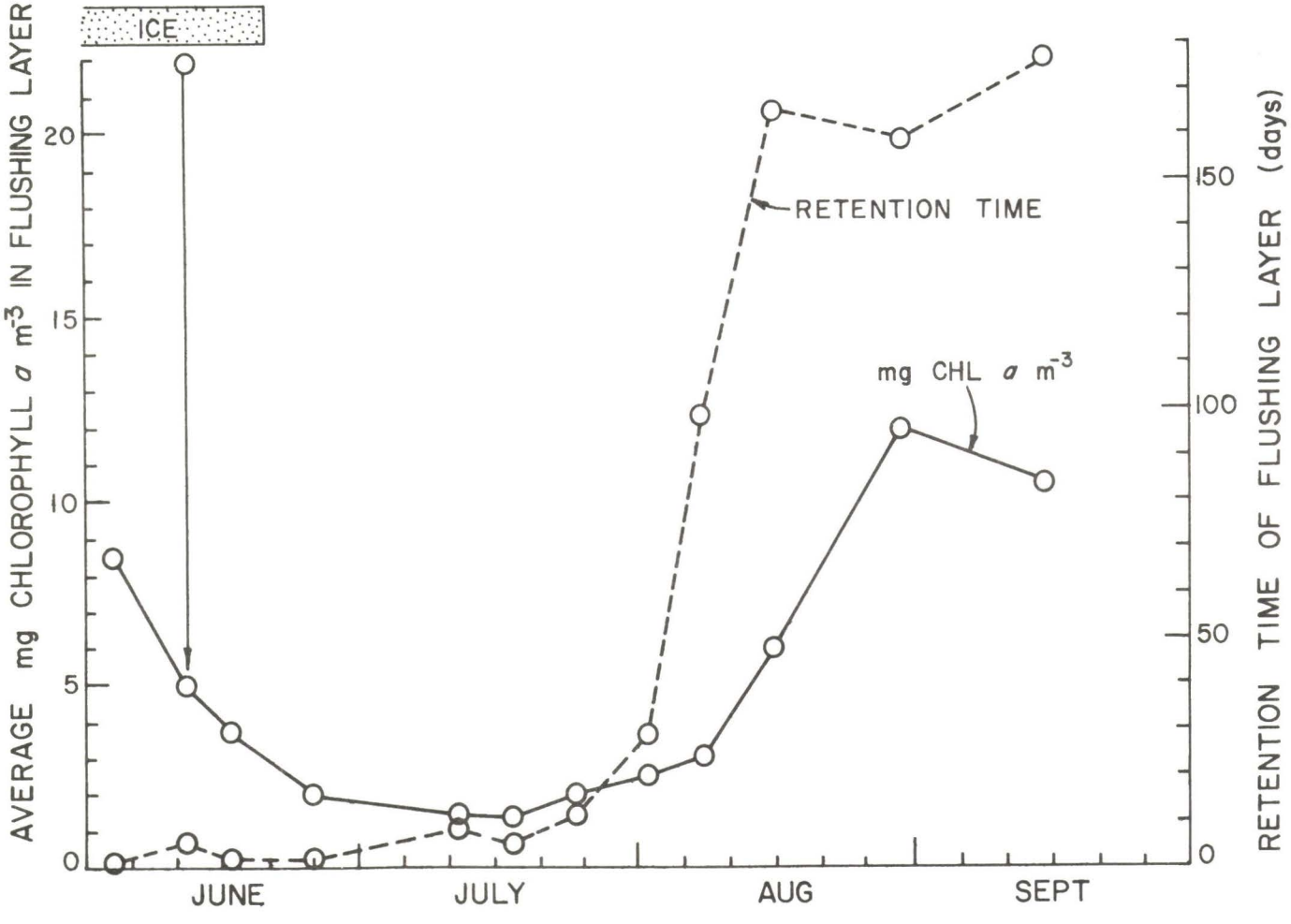

Fig. 48. Average chlorophyll a m^{-3} of flushing layer (solid line) and retention time of the flushing layer in days (dashed line) of Libby Lake in 1974. See text for explanation of arrow.

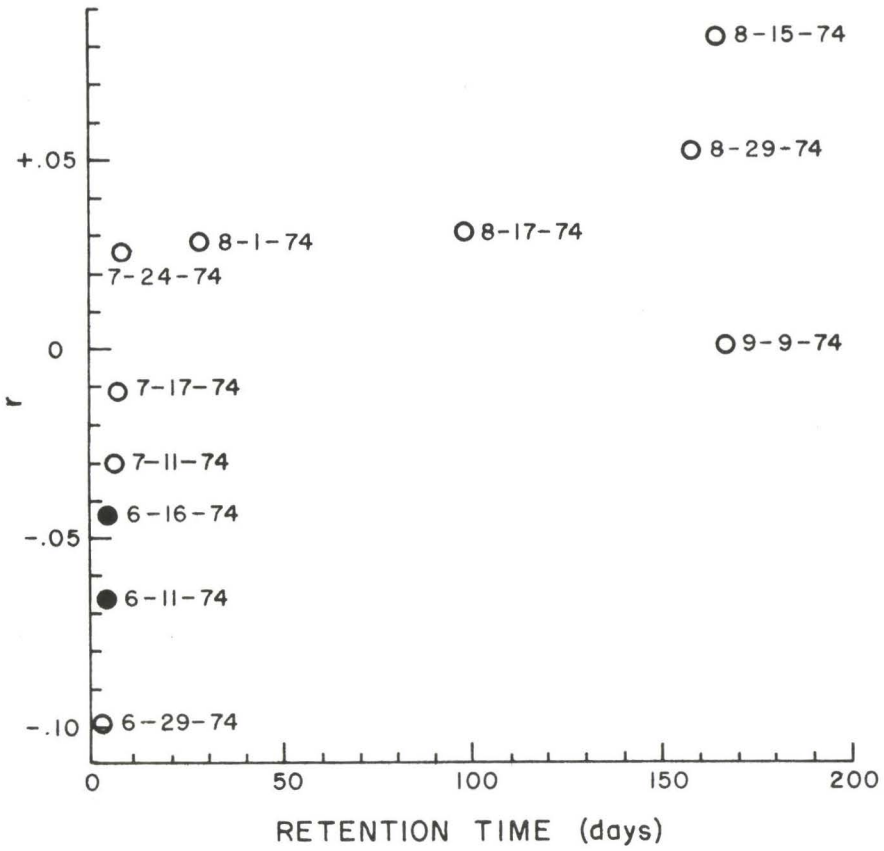

Fig. 49. The rate of population increase (r) of the flushing layer's phytoplankton plotted against retention time of the flushing layer. Solid dots represent data based in part on the mg chl a m^{-3} values from June 11, 1974. Data representing the solid dots were not used in statistical analyses.

is about 7.5 days (Fig. 48). When retention time is less than 7.5 days, algal biomass decreases (prior to about 17 July), while biomass increases at larger values of retention time.

The observed exception to a critical retention time of 7.5 days was on 11 June, when the only data were gathered that suggest that algal biomass is not lower in surface samples than at deeper depths (Fig. 46). The retention time had been very low for several weeks prior to 11 June, and the biomass should not have increased between 3 June and 11 June if the critical retention time is 7.5 days. It could be that the high biomass in the "flushing" layer on 11 June was due to the effect of short circuiting, and that we simply sampled at a location which was not flushing. However, there are no data to suggest this occurrence on any other date. We feel that the upper samples were taken at the wrong depth on 11 June. The lake was still ice covered, the thickness of the flushing layer was about 1 m, and we probably made a mistake in correcting for the thickness of the ice when lowering the water sampler. The biomass in the flushing layer on 11 June was therefore probably much less than the measured 22 mg chl *a* m^{-3}. The arrow for the 11 June date (Fig. 48) suggests a probable biomass of about 5 mg chl *a* m^{-3} as being more reasonable.

The critical retention time can also be evaluated by plotting r, the rate of population increase, versus retention time (Fig. 49). The value r was calculated from the equation

$$N_{s+1} = N_s e^{rt}$$

where N is algal biomass in the flushing layer (mg chl *a* m^{-3}), t is the time in days between sampling dates, and s represents a particular sampling date. Retention time was calculated by averaging the retention time of the two dates from which the biomass data were taken. The data points which necessitated using the probable biomass of 5 mg chl *a* m^{-3} on 11 June are indicated by solid circles on Fig. 49. However, they were not used in calculating the correlation statistics.

The correlation between r and retention time for data between 11 June and 24 July is highly significant (F significant at between the

0.01 and 0.005 level), and retention time accounts for 99 percent of the variation in r on these dates. After 24 July, when the volume flow of runoff had decreased to low levels, the regression changed drastically. The critical retention time is that which gives an r of zero; lower retention times then give a negative r, and algal biomass in the flushing layer decreases. The correlation equation gives a critical retention time of 7.02 days, which agrees which the estimate of 7.5 days from Fig. 48. Similar analyses of the data from 1972 and 1973 were not very conclusive, largely because biomass estimates were not made until the first week of July. The critical retention time calculated from the 1972 and 1973 data is about 10 days.

The values obtained for absolute primary productivity seemed somewhat high (Fig. 50; multiply the average mg C m^{-3} day^{-1} by 12 m to convert to areal units). However, the areal hypolimnetic oxygen deficit calculated from the dissolved oxygen data of 1972 is about 1 mg oxygen cm^{-2} $month^{-1}$, which is consistent with the ^{14}C estimates of primary production. There was considerable fixation of carbon at deeper depths because of the high algal biomass at these depths (Fig. 51). However, the depth at which the highest value of specific production (mg C mg chl $\underline{a}^{-1}$ day^{-1}) occurred varied from zero meters under the ice to a maximum of 3 m.

The calculated values of both XKP and PMAX were lowest under ice cover, and reached maximum values in July (Fig. 52A). The regression of XKP on water temperature and available incoming radiation was very significant (F significant at between the 0.005 and 0.001 level), and temperature and radiation accounted for 95.3 percent of the variation in XIP (see Fig. 52C, D). The regression equation is

$$XKP = 6.58 \cdot 10^{-5}(Ly\ day^{-1}) + 6.50 \cdot 10^{-3}(temperature) + 0.0125$$

The regressions of PMAX on available radiation (Fig. 52B) are:

$$PMAX - 2.78\ (temperature) + 4.63;\ R^2 = .698$$

$$\log\ (PMAX) = 0.061\ (temperature) + 0.841;\ R^2 = .754$$

The F statistic for each regression is significant at between the 0.25 and .01 level.

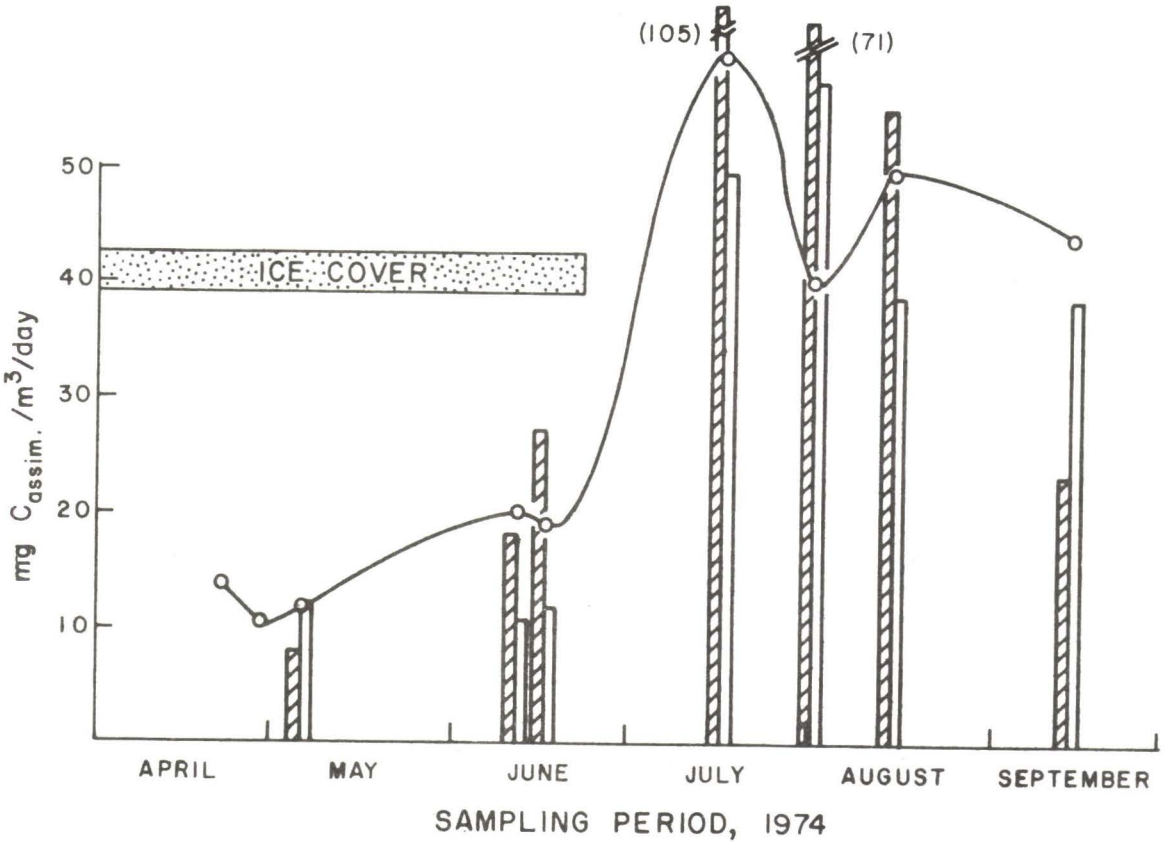

Fig. 50. Average absolute rates of primary production (ave. mg C m^{-3} day^{-1}) in Libby Lake, 1974 (solid line). Hatched bars represent mg C m^{-3} day^{-1} calculated from the model (eq. 2) with programmed values of XKP and PMAX, but with the actually observed average phytoplankton biomass. Unhatched bars represent average mg C m^{-3} day^{-1} calculated from the model (eq. 2) using actually observed values of XKP, PMAX and average phytoplankton biomass.

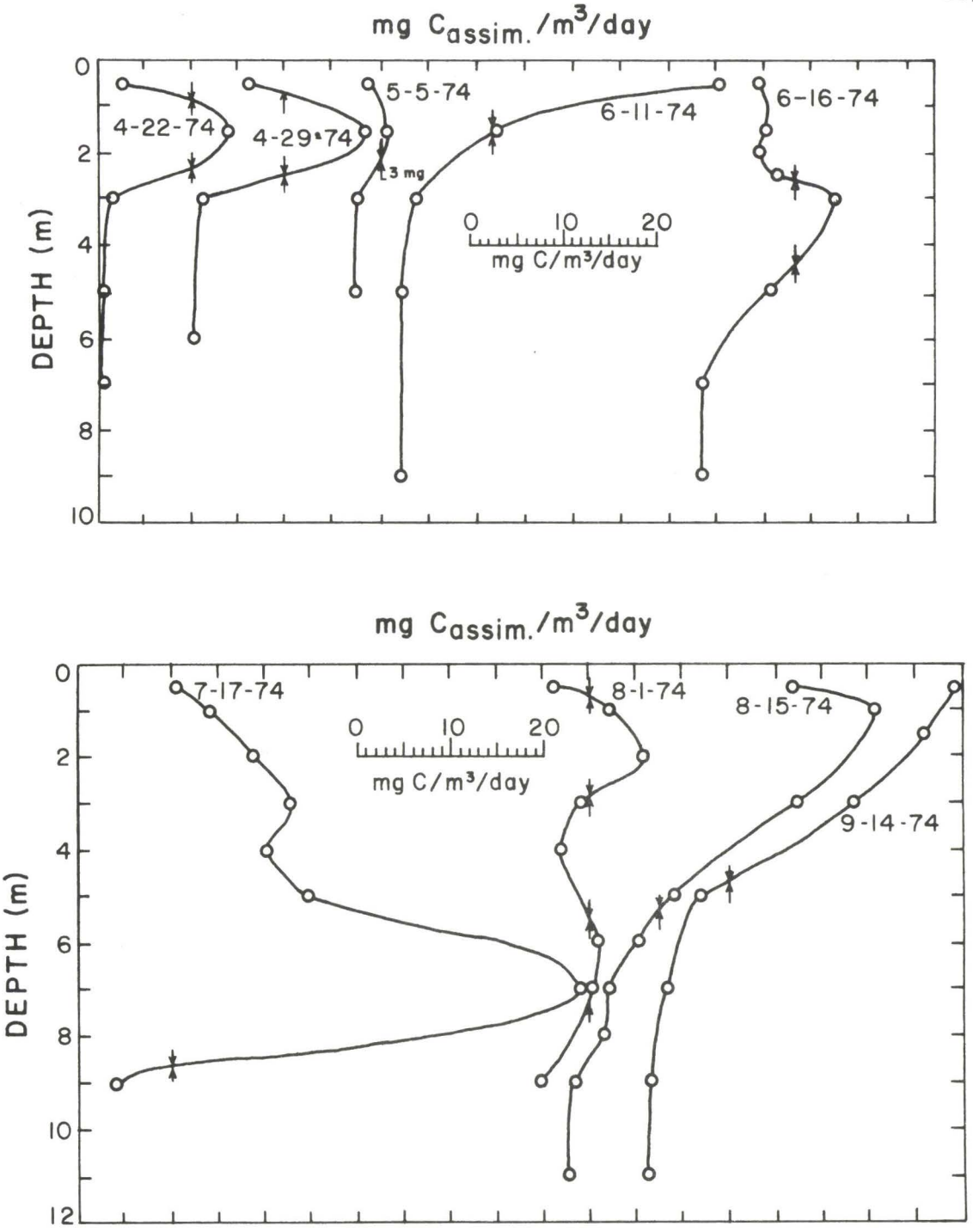

Fig. 51. Absolute rates of primary production (mg C m^{-3} day^{-1}) versus depth in meters for 1974 sampling dates in Libby Lake. Unless otherwise indicated the arrows on each curve represent a value of 10 mg C $m^{-3}day^{-1}$. A scale of mg C m^{-3} day^{-1} is indicated on the graph. The lake was ice covered through the sampling date of June 16, 1974.

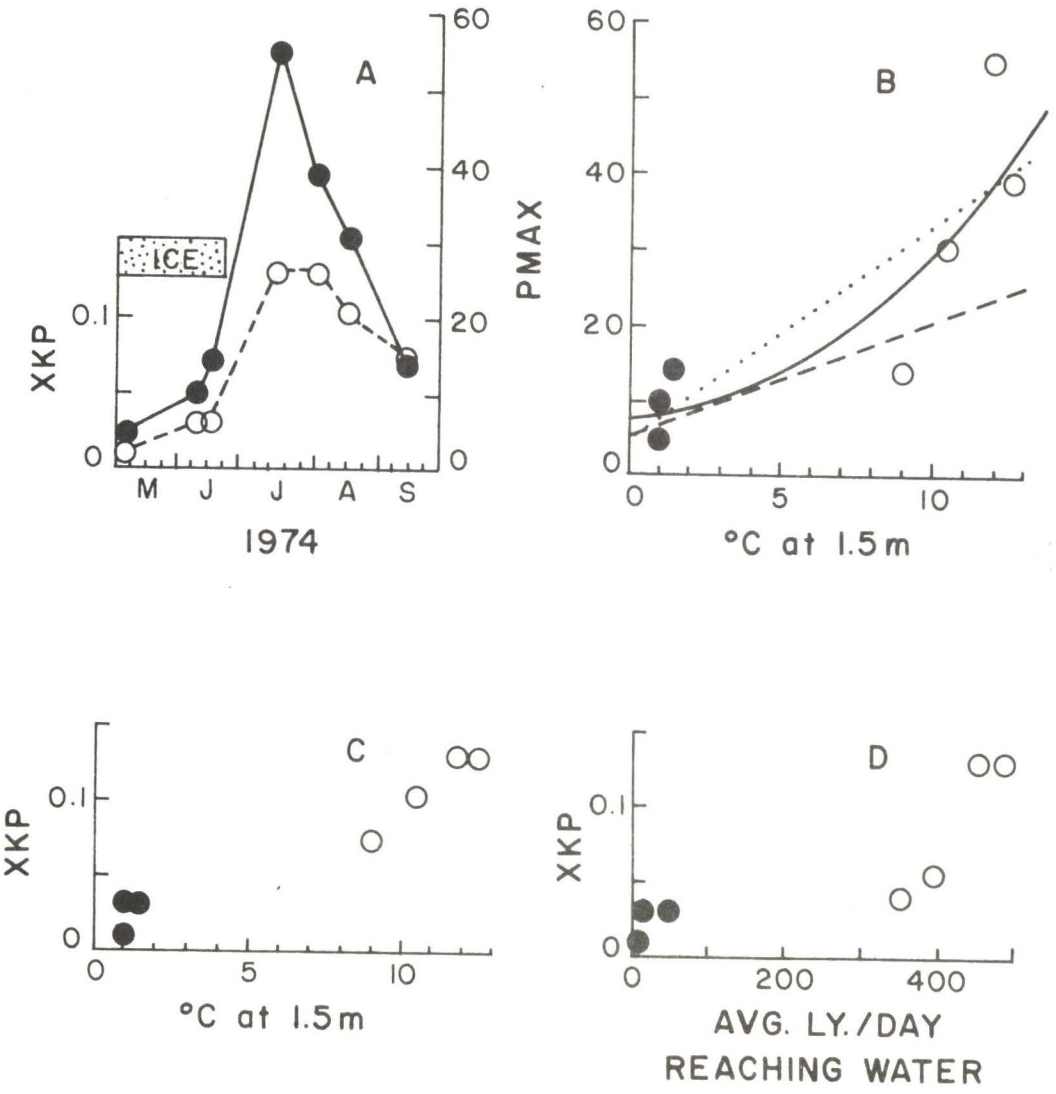

Fig. 52. A. Values of XKP (dashed line) and PMAX (solid line) calculated from the ^{14}C experiments of 1974. B. Values of PMAX plotted versus water temperature (°C) of the flushing layer. Solid circles represent data from the ice covered period, open circles data from the ice free period. The dashed line represents the regression of PMAX on water temperature used in the model. The solid line represents the regression of log(PMAX) on temperature for the data. The dotted line represents a linear regression of PMAX on temperature for the data. C. Values of XKP plotted versus water temperature (°C) of the flushing layer. Solid circles represent data from the ice covered period, open circles data from the ice free period. D. Values of XKP plotted versus average langleys per day reaching the surface of the water. Solid circles represent data from the ice covered period, open circles data from the ice free period.

The following procedure was used to evaluate the effect of several factors on an average specific growth rate in the flushing layer of the lake. The depth below the surface, where the value of mg C mg chl $\underline{a}^{-1}$ day^{-1} equaled PMAX/2, was calculated for each ^{14}C experiment. These calculated depths always fell within the flushing layer. The mg C m^{-2} day^{-1} from these depths to the surface was calculated and divided by the average mg chl $\underline{a}$ m^{-3} in the flushing layer. This quantity, with units of average mg C mg chl $\underline{a}^{-1}$ day^{-1}, was termed the birth rate index. This quantity was correlated (1) separately with linear and nonlinear measures of retention time, available incoming radiation, temperature of the flushing layer, and an index of probable zooplankton grazing intensity (grazing units taken from ordinate of Fig. 45G; see Fig. 53) (2) with the four combinations of linear and nonlinear measures of retention time and radiation, and (3) with the eight combinations of linear and nonlinear retention time, radiation, and grazing intensity. All four multiple correlations with retention time and radiation as independent variables were significant at the 0.025 level. Two of the eight multiple correlations with retention time, radiation and grazing as independent variable were significant at the 0.05 level or better. Hence even though there are few data points (the data from 11 June were not used for the reasons discussed previously, and volume flow data were not available for 5 May, 1974), the correlations explain a large amount of the variation of the flushing layer's birth rate index.

The rate of population increase (r) is the difference between birth and death rates:

$$r = b - d$$

and

$$d = b - r$$

The calculated measures of r and birth rate (birth rate index, BRI) were used to calculate a death rate index (DRI):

$$DRI = \text{death rate index} = (BRI - (100r) + 7$$

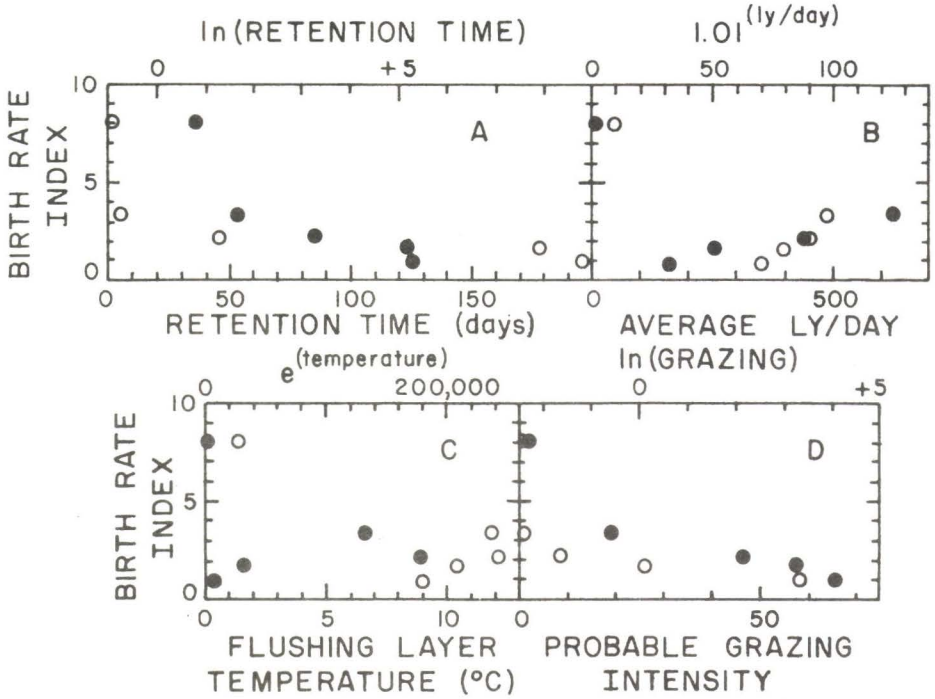

Fig. 53. A. Birth rate index plotted versus retention time in days of the flushing layer, 1974. Open circles, abscissa scale linear; solid circles, abscissa scale of ln(retention time). B. Birth rate index plotted versus average langleys per day reaching the surface of the water, 1974. Open circles, abscissa scale linear; solid circles, abscissa scale of $1.01^{(\text{langleys per day})}$. C. Birth rate index plotted against water temperature (°C) of the flushing layer, 1974. Open circles, abscissa scale linear; solid circles, abscissa scale of $e^{(\text{temperature})}$. D. Birth rate index plotted versus probable grazing intensity in 1974 (grazing units from ordinate of Fig. 14G). Open circles, abscissa scale linear; solid circles, abscissa scale of ln (probable grazing intensity).

The formula was chosen for convenience as one which would give values from about 0.5 to 20. It is termed DRI since the experimental measures of r and birth rate are in different units, and the actual death rate could not be calculated with any precision.

The DRI was correlated (1) separately with linear and nonlinear forms of the retention time and grazing intensity data (Fig. 54) and (2) with the four combinations of linear and nonlinear forms of retention time and grazing intensity data. The two independent variables of ln (retention time) and grazing together accounted for 94 percent of the variation in DRI. The F statistic was only significant at the 0.1 level, thus, although there appears to be a relationship between these three variables, the exact form of the correlation model probably should not be trusted for predictive purposes.

Simulation Results

Model with all loss rates (RP = .15, SP = 5m/day, flushing at 1972 time and levels, grazing maximum = 0.078 $gC/m^3/day$).

Over the range of variables investigated (Tables 56 and 57), the model generated specific gross production rates of 0.09 to 0.46 gC/gC/day and absolute gross production rates of 0 to 197 $mgC/m^3/day$. When respiration was increased or PMAX was decreased, absolute gross production decreased but specific gross production increased. An increase in respiration or a decrease in PMAX also caused a decrease in the maximum phytoplankton standing crop and in the standing crop at the end of the year (Table 58, Fig. 55).

A comparison of the phytoplankton standing crop generated by the model and the standing crop from 1972 Libby Lake data is shown in Fig. 56. Chlorophyll data were converted to gC/m^3 using a conversion factor of 30 (Strickland 1960). The shape of the phytoplankton standing crop versus time curve generated by the model with all losses is the same as that given by data from Libby Lake. However, in most cases the standing crop generated by the model was lower than that found in the lake. The 1972 chlorophyll data were the most reliable data on phytoplankton standing crop in Libby Lake.

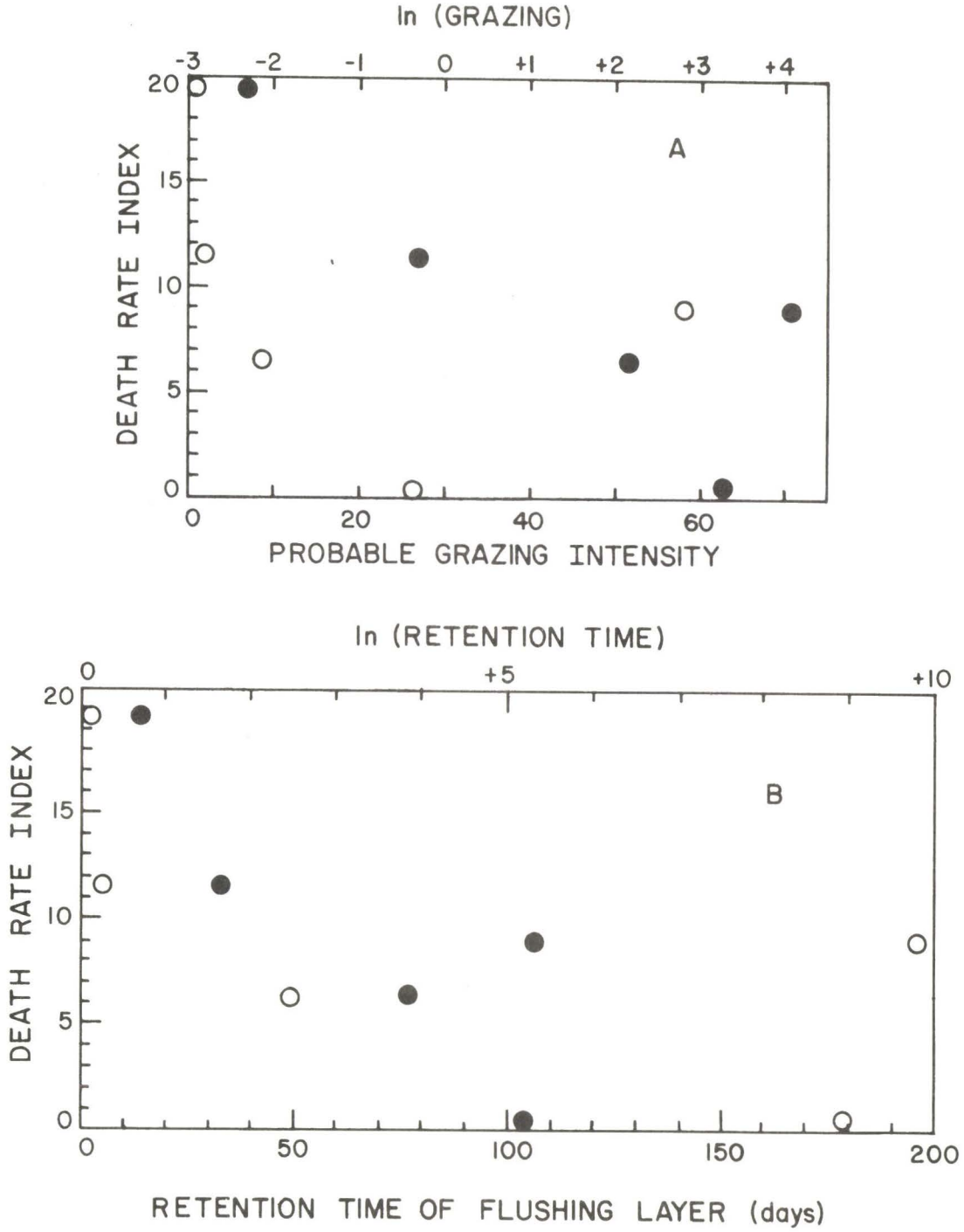

Fig. 54. A. Death rate index plotted versus probable grazing intensity (grazing units from ordinage of Fig. 14G). Open circles, abscissa scale linear; solid circles, abscissa scale of ln(probable grazing intensity). B. Death rate index plotted versus retention time in days of the flushing layer. Open circles, abscissa scale linear; solid circles, abscissa scale of ln (retention time).

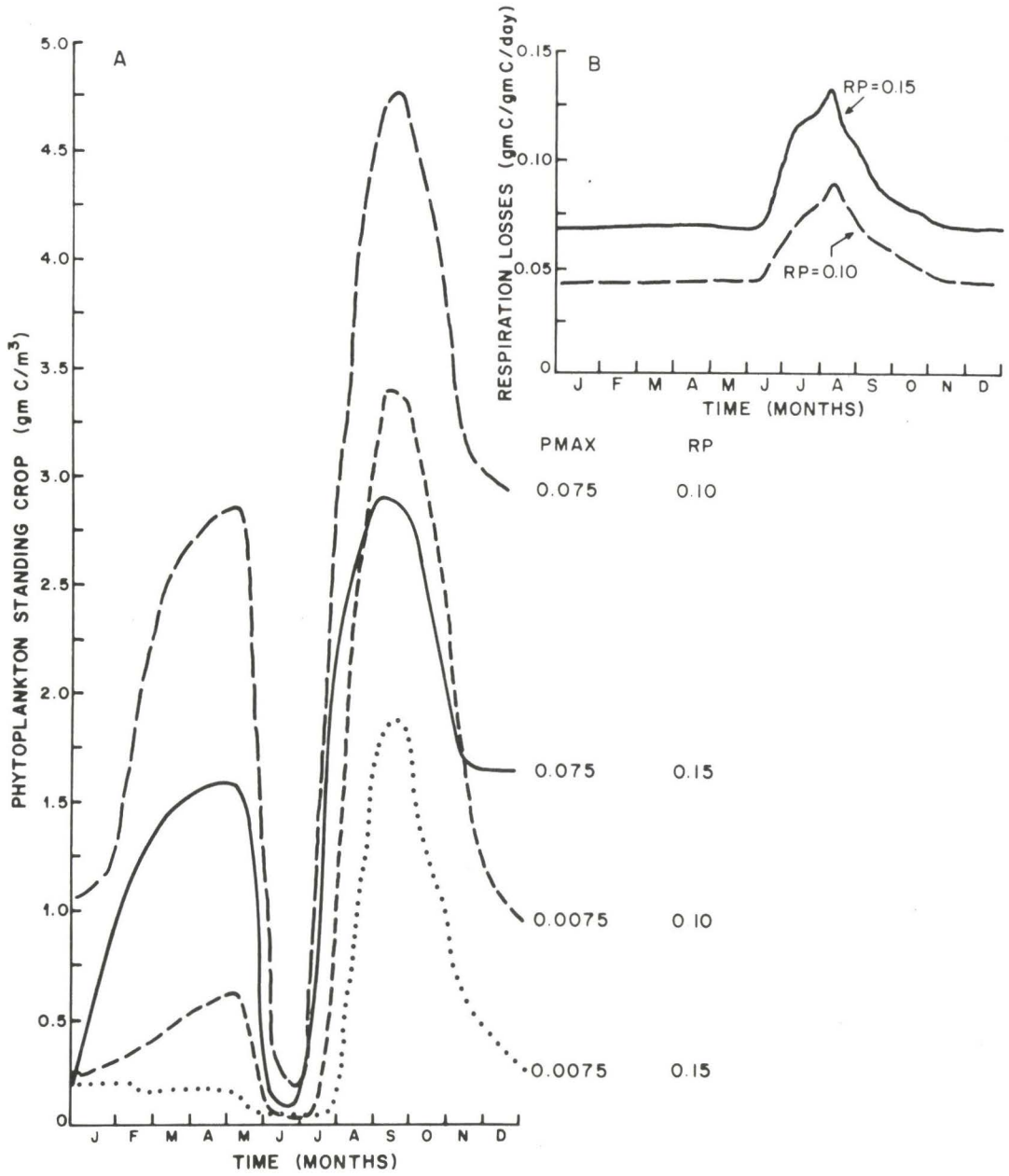

Fig. 55. A. Effects of changing PMAX (maximum rate of photosynthesis at light saturation) and RP (respiration loss at 15°C) on the phytoplankton biomass generated by the model. B. Respiration losses (g C/g C/day at RP values of 0.10 and 0.15.

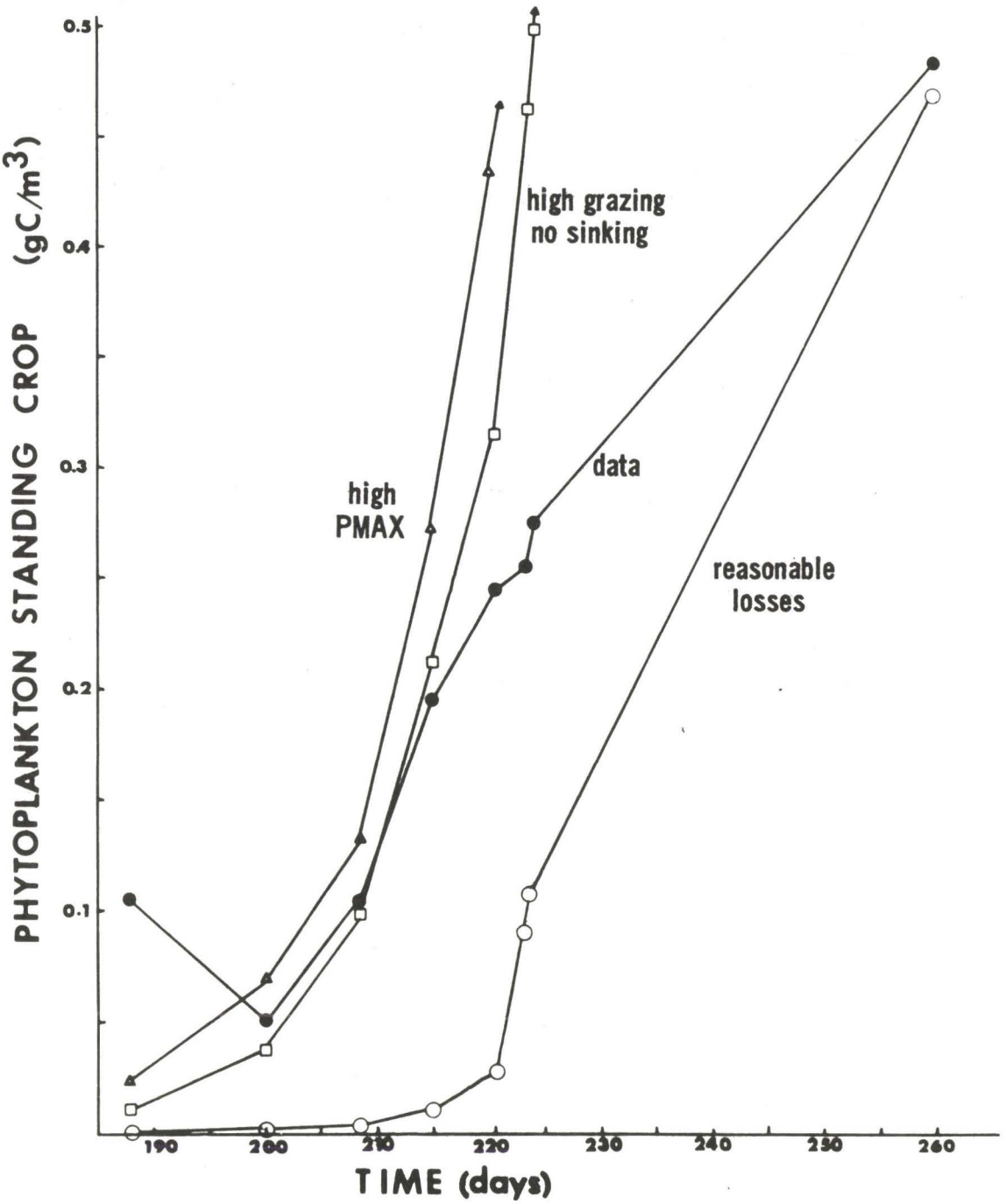

Fig. 56. Comparison of phytoplankton biomass (gC/m^3) generated by the model with the 1972 biomass data from Libby Lake (chlorophyll a/m^3 converted to gC/m^3). The solid dots indicate values from 1972 chlorophyll a data; the open circles indicate values generated by the model with all loss rates at reasonable levels (RP = 0.15, sinking rate = 0.5 m/day, flushing = 1972 timing and level, and grazing = 0.08 gC/m^3/day); the squares indicate model results with high grazing losses and no sinking losses; and the triangles indicate model results with an increased PMAX (i.e., PMAX twice that of other runs).

TABLE 56. The effects of changing runoff parameters on phytoplankton and zooplankton with all loss rates in the model. Output parameters considered are magnitude and time of occurrence of fall phytoplankton peak, phytoplankton production rates, phytoplankton standing crop at the year's end; and maximum zooplankton standing crop and grazing rate, and zooplankton standing crop at the year's end.

	Runoff Parameter Varied						
	None (1972 parameters)	Time (days)	Magnitude (% 1972 volume flow)			Shape Factor (See Table VII)	
Output parameters		+15	+30	+43	+86	2	10
A. Phytoplankton parameters							
1. Fall peak							
a. Standing crop (gC/m^3)	0.48	0.48	0.48	0.86	0.71	0.42	0.43
b. Day of year	254	270	284	259	287	260	258
2. Standing crop at year's end (gC/m^3)	0.02	0.02	0.03	0.02	0.02	0.02	0.02
3. Range of PSYN ($gC/m^3/day$)	0.000 to 0.149	0.000 to 0.149	0.000 to 0.149	0.000 to 0.169	0.000 to 0.105	0.000 to 0.108	0.001 to 0.116
4. Range of production (gC/gC/day)	0.1227 to 0.4124	0.1227 to 0.4124	0.1227 to 0.4125	0.1155 to 0.4522	0.1104 to 0.4584	0.1232 to 0.3892	0.1233 to 0.3874
B. Zooplankton parameters							
1. Maximum standing crop (gC/m^2)	0.23	0.23	0.23	0.17	0.09	0.18	0.18
2. Standing crop at year's end (gC/m^2)	0.01	0.02	0.02	0.02	0.02	0.01	0.01
3. Maximum grazing ($gC/m^3/day$)	0.078	0.078	0.078	0.048	0.021	0.054	0.058

TABLE 57. The effects of changing loss rates on phytoplankton and zooplankton with all loss rates in the model. Reasonable loss rates are considered to be respiration loss of .15 at 15°C, sinking rate of 0.5m/day, flushing at 1972 time and level, and grazing losses of 0.07 to 0.08 $gC/m^3/day$. Grazing losses, however, vary with other loss rates. Output parameters considered are phytoplankton fall peak magnitude and timing, phytoplankton production rates, phytoplankton standing crop at year's end, maximum zooplankton standing crop, and zooplankton standing crop at year's end.

	Loss Rate Varied					
	None (all reasonable)	Respiration (RP in gC/gC/day)		Sinking (m/day)		Grazing ($gC/m^3/day$)
Output parameters		0.10	0.20	0.25	1.00	0.045
A. Phytoplankton parameters						
1. Fall peak						
a. Standing crop (gC/m^3)	0.48	0.98	0.44	0.70	0.44	0.68
b. Day of year	254	284	250	287	272	261
2. Standing crop at year's end (gC/m^3)	0.02	0.31	0.01	0.20	0.004	0.08
3. Range of PSYN ($gC/m^3/day$)	0.000 to 0.149	0.000 to 0.197	0.000 to 0.117	0.000 to 0.172	0.000 to 0.090	0.000 to 0.149
4. Range of production (gC/gC/day)	0.1227 to 0.4124	0.0904 to 0.4076	0.1308 to 0.4474	0.0983 to 0.4081	0.1310 to 0.4574	0.1140 to 0.4175
B. Zooplankton parameters						
1. Maximum standing crop (gC/m^2)	0.23	0.31	0.17	0.27	0.10	0.45
2. Standing crop at year's end ($gC/m^2/day$)	0.01	0.07	0.005	0.06	0.002	0.10
3. Maximum grazing ($gC/m^3/day$)	0.078	0.108	0.049	0.093	0.024	0.045

TABLE 58. The effects of changing PMAX, maximum photosynthesis at light saturation, and RP, respiration losses at 15°C, on the phytoplankton. Output parameters considered are magnitude and time of occurrence for spring and fall peaks, production rates, and standing crop at year's end.

	PMAX			
	0.075		0.0075	
	RP		RP	
Output parameters	0.10	0.15	0.10	0.15
A. Fall peak				
1. Standing crop (gC/m^3)	4.7	2.9	3.4	1.8
2. Day of year	264	260	260	263
B. Spring peak				
1. Standing crop (gC/m^3)	3.0	1.6	0.6	none
2. Day of year	135	142	135	none
C. Range of Psyn (gC/m^3/day)	0.019 to 0.495	0.009 to 0.399	0.001 to 0.327	0.000 to 0.215
D. Range of production (gC/gC/day)	0.038 to 0.279	0.056 to 0.316	0.026 to 0.318	0.039 to 0.340
E. Standing crop at year's end (gC/m^3)	2.92	1.60	0.96	0.31

The 1972 cell count data were subject to error introduced by two conversion factors (i.e. numbers to volume, and volume to carbon), and sampling and counting errors. The 1973 chlorophyll data were not reliable because of problems of an undertermined nature with the spectrophotometer.

Effects of changing runoff parameters with only respiration and flushing in the model

A change in the time of occurrence of runoff caused an equal change in the time of occurrence of the fall and spring phytoplankton peaks (Table 59, Fig. 57). The rate of production and the magnitude of the fall peak of phytoplankton did not change with changes in the time of occurrence of runoff. However, both the spring peak of phytoplankton and the standing crop at the year's end increased as runoff occurred later in the year.

The magnitude of the phytoplankton standing crop was inversely related to the total volume flow of runoff. Considering the 55 year mean of volume flow as a reference point, the fall peak of phytoplankton standing crop changed as follows when volume flow was varied: volume flow increased 50 percent, fall peak decreased 14 percent; volume flow decreased 50 percent, fall peak increased 9 percent; volume flow increased 100 percent, fall peak decreased 52 percent (Table 60 and Fig. 58).

Changing the shape of the runoff versus time curve also changed the total volume flow of runoff (Table 61 and Fig. 59). As the runoff versus time curve became broader the effect of runoff on the phytoplankton became less dramatic (i.e. the phytoplankton minimum at the end of June became higher). However, the effect on the phytoplankton maximum standing crop became greater (i.e. the fall peak is lower). Comparing the inset of Fig. 59 with Fig. 43, however, shows that the curves generated by the model for low volume flows did not fall off as rapidly as they did in nature.

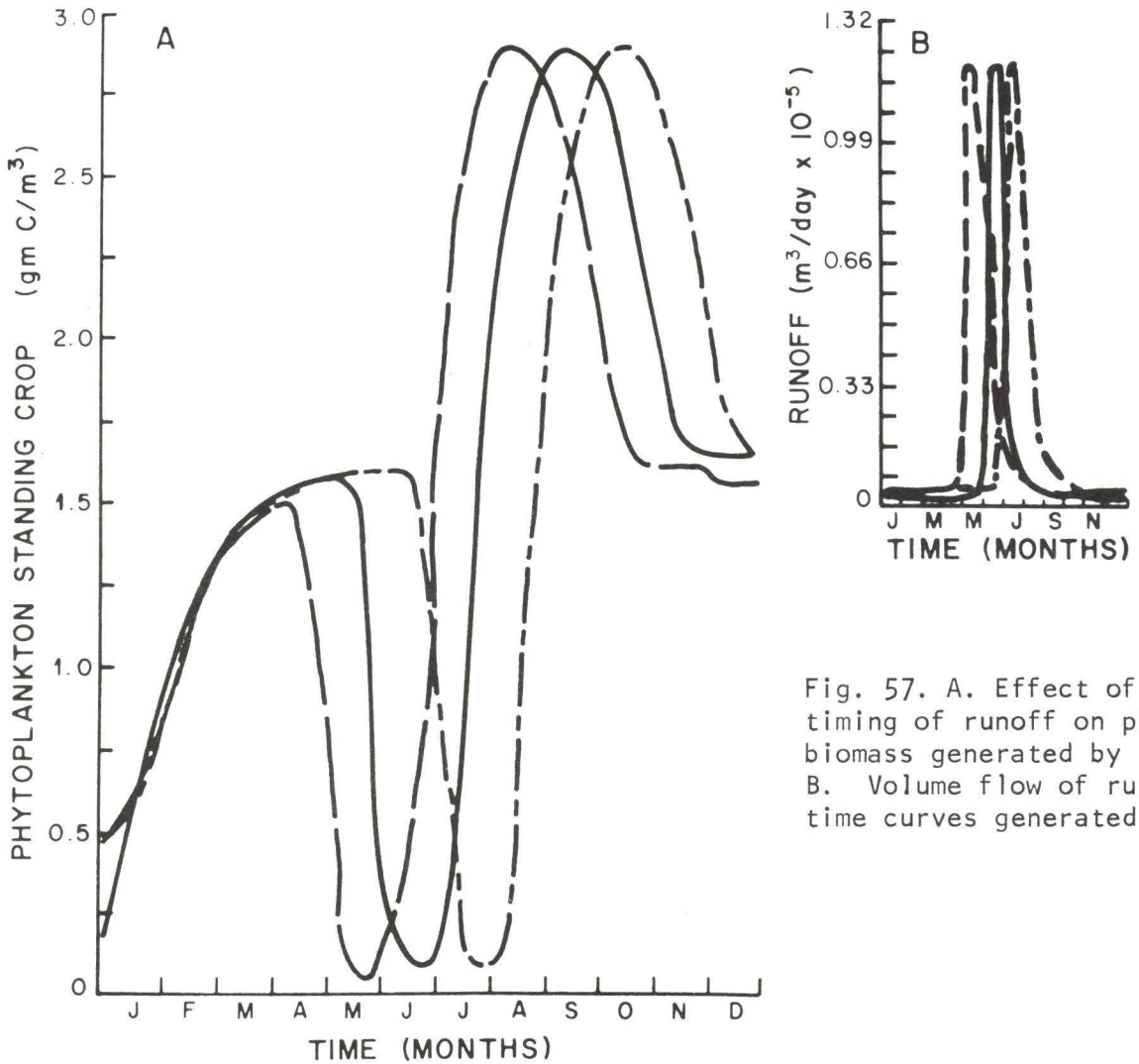

Fig. 57. A. Effect of changing the timing of runoff on phytoplankton biomass generated by the model. B. Volume flow of runoff versus time curves generated by the model.

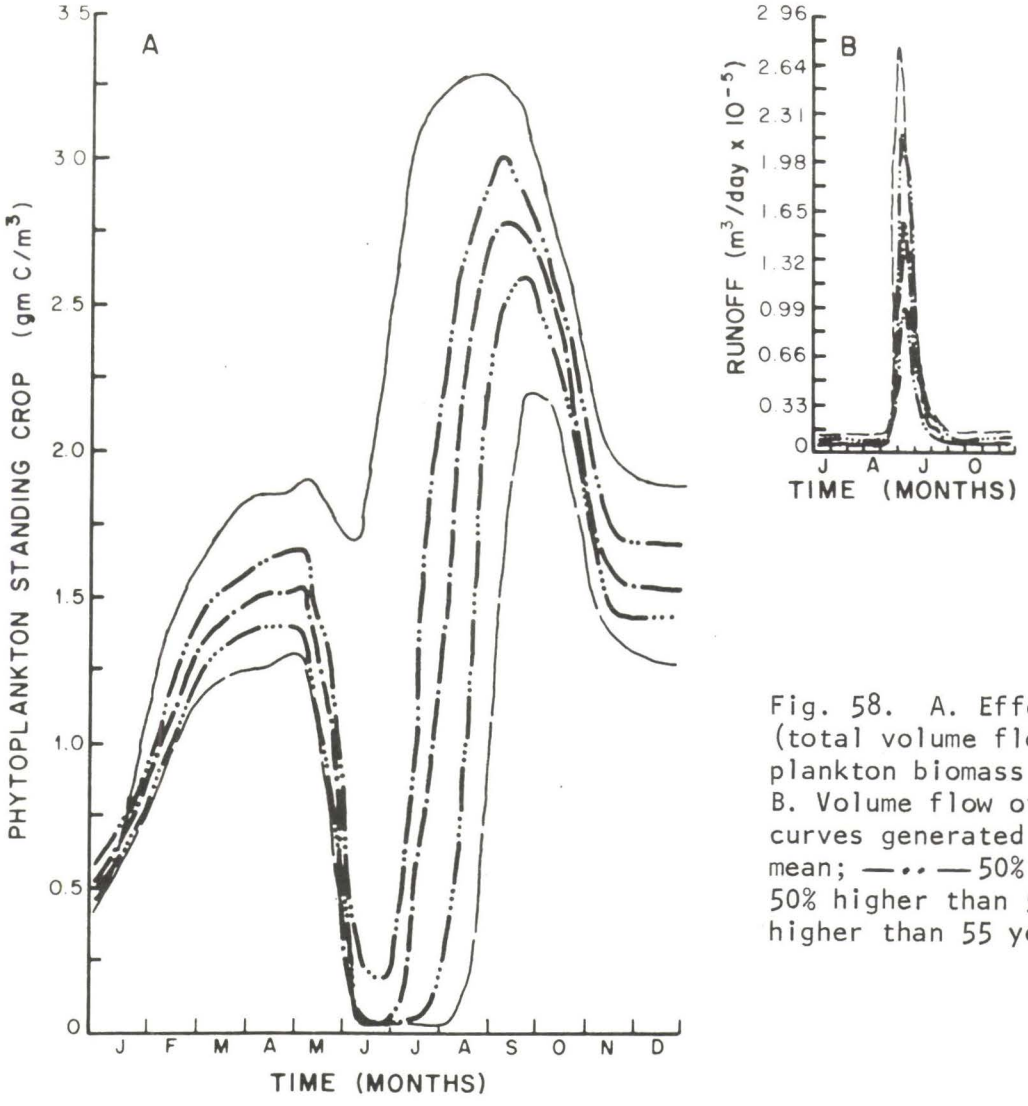

Fig. 58. A. Effect of changing the magnitude (total volume flow, m^3) of runoff on the phytoplankton biomass (gC/m^3) generated by the model. B. Volume flow of runoff (m^3/day) versus time curves generated by the model. —•— 55 year mean; —••—50% lower than 55 year mean; —•••— 50% higher than 55 year mean; — — 100% higher than 55 year mean; ——— no runoff.

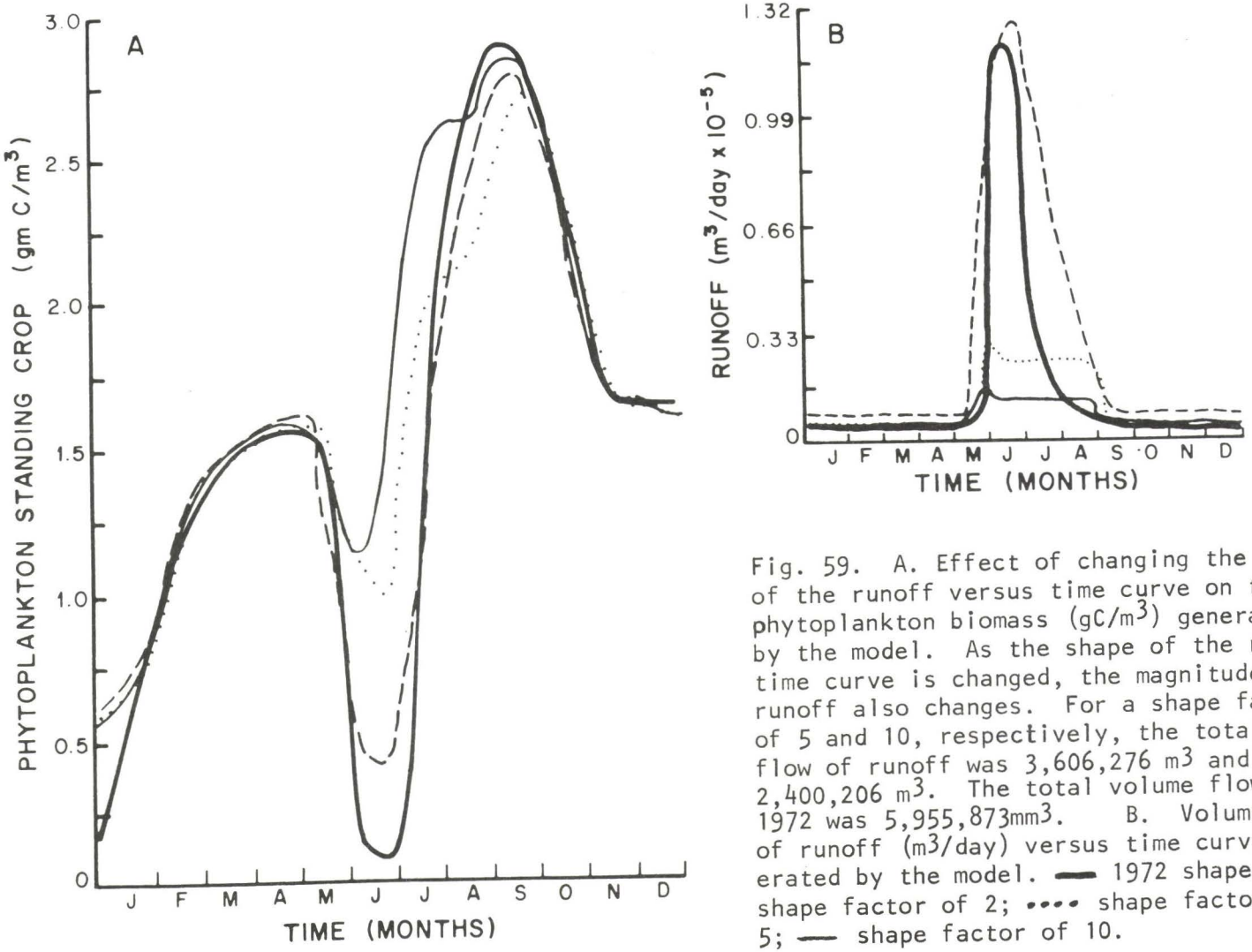

Fig. 59. A. Effect of changing the shape of the runoff versus time curve on the phytoplankton biomass (gC/m^3) generated by the model. As the shape of the runoff time curve is changed, the magnitude of runoff also changes. For a shape factor of 5 and 10, respectively, the total volume flow of runoff was 3,606,276 m^3 and 2,400,206 m^3. The total volume flow for 1972 was 5,955,873mm^3. B. Volume flow of runoff (m^3/day) versus time curves generated by the model. ▬ 1972 shape; – – – shape factor of 2; •••• shape factor of 5; ▬ shape factor of 10.

TABLE 59. The effects of changing the time of occurrence of spring runoff on the phytoplankton. Output parameters considered are magnitude and time of occurrence for spring and fall peaks, production rates, and standing crop at year's end.

Output parameters	Time shift from 1972 time of occurrence (days)				
	-30	-15	0	+15	+30
A. Fall peak					
1. Standing crop (gC/m^3)	2.9	2.9	2.9	2.9	2.9
2. Day of year	230	245	260	275	290
B. Spring peak					
1. Standing crop (gC/m^3)	1.55	1.57	1.58	1.59	1.59
2. Day of year	112	127	142	157	172
C. Range of PSYN (gC/m^3/day)	0.009 to 0.399	0.009 to 0.399	0.009 to 0.399	0.009 to 0.399	0.009 to 0.399
D. Range of production (gC/gC/day)	0.056 to 0.316	0.056 to 0.316	0.056 to 0.316	0.056 to 0.315	0.056 to 0.315
E. Standing crop at year's end (gC/m^3)	1.59	1.60	1.60	1.60	1.61

TABLE 60. The effect of changing the magnitude (total volume flow, m^3/day) of runoff on the phytoplankton. Output parameters considered are the magnitude of runoff, the maximum flushing rate, the magnitude and time of occurrence of the fall and spring phytoplankton peaks, production rates and the standing crop at the end of the year.

Runoff parameters	MAGNITUDE					
1. Total volume flow (m^3)	4,228,633	5,955,873	8,516,874	11,077,858	12,745,543	17,033,456
2. Percent change from 55 year mean	-50	-30	0	+30	+50	+100
3. Maximum flushing loss (gC/gC/day)	0.17	0.24	0.34	0.44	0.51	0.68
Output parameters						
A. Fall peak						
1. Standing crop (gC/m^3)	2.996	2.894	2.739	2.541	2.342	1.324
2. Percent change from value for 55 year mean volume flow	+9	+6	0	-7	-14	-52
3. Day of year	259	260	262	266	273	299
B. Spring peak						
1. Standing crop (gC/m^3)	1.658	1.581	1.474	1.375	1.314	1.168
2. Day of year	142	142	142	142	142	142
C. Range of PSYN (gC/m^3/day)	0.024 to 0.411	0.009 to 0.399	0.001 to 0.363	0.000 to 0.305	0.000 to 0.268	0.000 to 0.136
D. Range of production (gC/gC/day)	0.0542 to 0.2644	0.0556 to 0.3155	0.0577 to 0.3884	0.0599 to 0.4102	0.0614 to 0.4112	0.0709 to 0.4585
E. Standing crop at year's end						
1. gC/m^3	1.677	1.599	1.491	1.390	1.327	1.155
2. Percent change from value for 55 year mean volume flow	+12	+7	0	-7	-11	-23

TABLE 61. The effect of changing the shape of the runoff versus time curve on the phytoplankton. Output parameters considered are total volume flow of runoff, maximum flushing loss (gC/gC/day), the magnitude and time of occurrence of fall and spring phytoplankton peaks, production rates and standing crop at the end of the year. As the shape factor increases, the total volume flow of runoff decreases and the runoff versus time curve becomes broader.

	Factor by which shape was changed from 1972 data (shape factor)				
Output parameters	none	2	3.65	5	10
A. Runoff					
1. Total volume flow (m^3)	5,955,873	5,206,701	4,220,890	3,606,276	2,400,206
2. Maximum flushing loss (gC/gC/day)	0.24	0.12	0.06	0.05	0.02
B. Fall peak					
1. Standing crop (gC/m^3)	2.89	2.81	2.72	2.72	2.84
2. Day of year	260	265	268	268	263
C. Spring peak					
1. Standing crop (gC/m^3)	1.58	1.58	1.58	1.58	1.58
2. Day of year	142	142	142	142	142
D. Range of PSYN (gC/m^3/day)	0.009 to 0.399	0.028 to 0.380	0.058 to 0.371	0.067 to 0.379	0.028 to 0.409
E. Range of production (gC/dC/day)	0.0556 to 0.3155	0.0557 to 0.2495	0.0558 to 0.1926	0.0558 to 0.1798	0.0556 to 0.1560
F. Standing crop at year's end (gC/m^3)	1.60	1.60	1.60	1.60	1.60

Changing the temperature during runoff had no effect on the phytoplankton standing crop or on production rates. Even when radical changes were allowed (e.g. volume flow of runoff 100 percent greater than the 55 year mean and runoff water temperatures less than 0°C), there were no changes caused by temperature in the standing crop levels or in the range of production rates during the year.

Short circuiting effects occur only during the period of runoff. As short circuiting becomes more important, flushing losses to the phytoplankton decrease. A value for short circuiting was calculated from the contour map of Libby Lake assuming a mean channel depth of 2.4 m, a mean width of 81 m, and a channel length of 462 m. The maximum volume of the lake flushed in one day was then 79,104 m^3/day. This represents a maximum flushing loss to the phytoplankton of 0.126 gC/gC/d. If no short circuiting occurred the minimum phytoplankton standing crop was 0.0491 gC/m^3. If short circuiting occurred at the rate calculated above, the minimum phytoplankton standing crop increased approximately four times to 0.1692 gC/m^3. If short circuiting occurred at half the calculated rate, the minimum phytoplankton standing crop increased approximately ten times to 0.5170 gC/m^3 (Table 62 and Fig. 60).

Effects of changing sinking and grazing losses with respiration and flushing in the model

In general an increase in the sinking rate caused a decrease in the phytoplankton standing crop at all times of the year (Table 63 and Fig. 61). A sinking rate of 4 m/day almost eliminated the phytoplankton. A sinking rate of 1 m/day eliminated the spring phytoplankton peak and lowered the fall peak from 2.9 gC/m^3 to 0.82 gC/m^3. With a sinking rate of 0.5 m/day a spring peak again occurred, and the fall peak was lowered from 2.9 gC/m^3 to 1.7 gC/m^3.

An increase in the phytoplankton losses via zooplanktonic grazing also decreased the phytoplankton standing crop at all times of the year (Table 64 and Fig. 62). High grazing losses eliminated the spring peak and lowered the fall phytoplankton peak from 2.9 gC/m^3

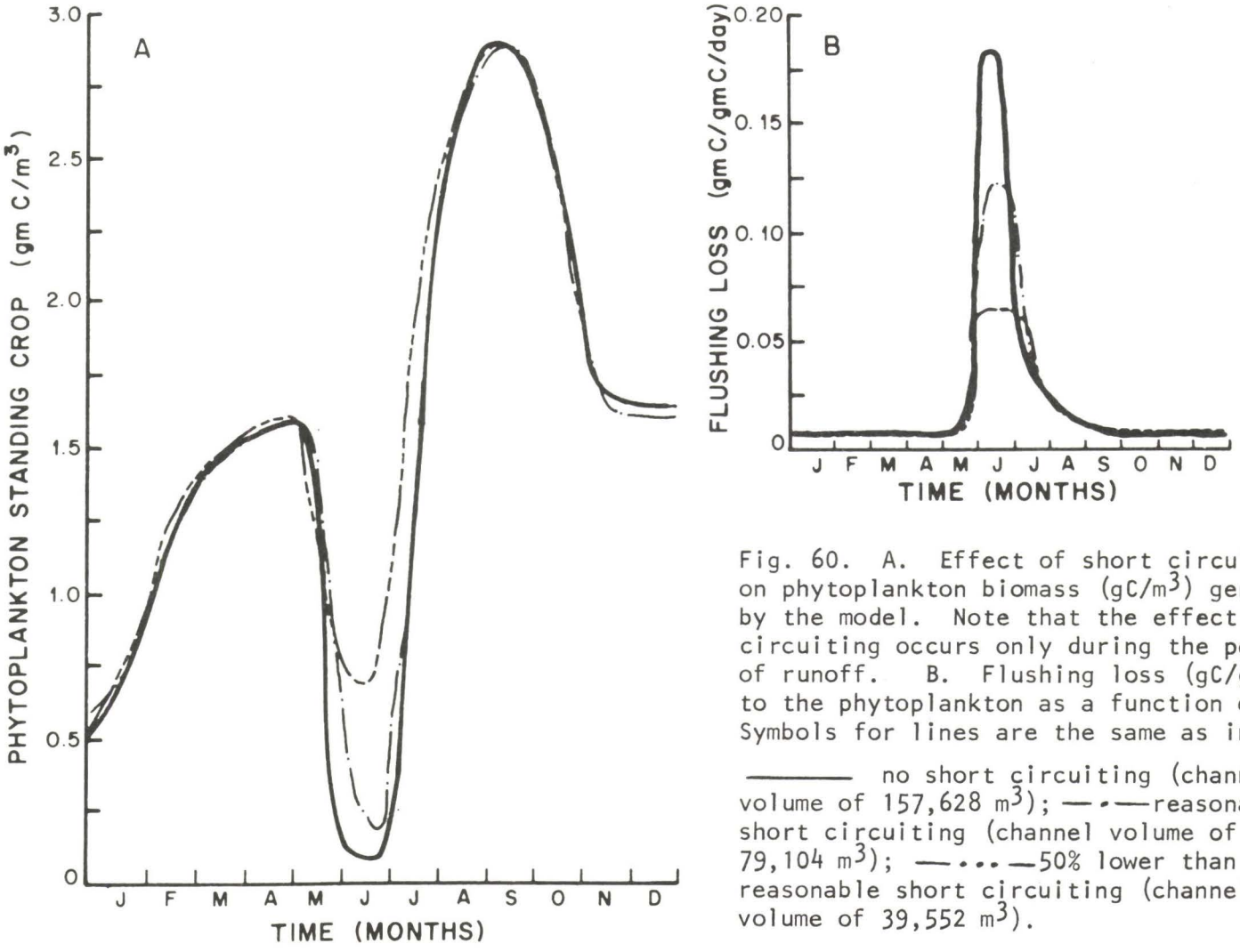

Fig. 60. A. Effect of short circuiting on phytoplankton biomass (gC/m^3) generated by the model. Note that the effect of short circuiting occurs only during the period of runoff. B. Flushing loss (gC/gC/day) to the phytoplankton as a function of time. Symbols for lines are the same as in A.

——— no short circuiting (channel volume of 157,628 m^3); —·— reasonable short circuiting (channel volume of 79,104 m^3); —···— 50% lower than reasonable short circuiting (channel volume of 39,552 m^3).

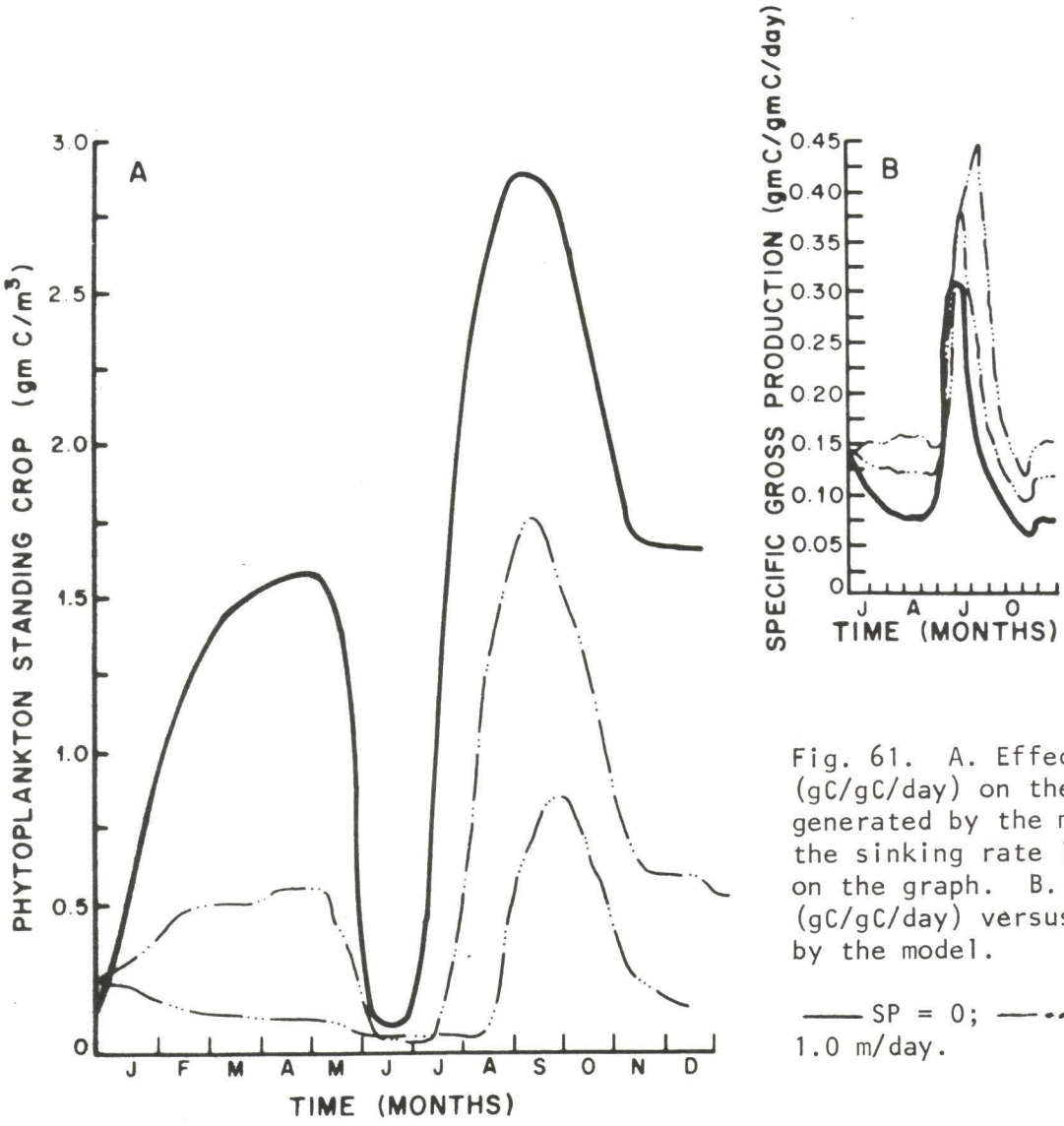

Fig. 61. A. Effect of sinking losses (gC/gC/day) on the phytoplankton biomass generated by the model. Values for SP, the sinking rate in m/day, are indicated on the graph. B. Specific production (gC/gC/day) versus time curves generated by the model.

—— SP = 0; —·—·—SP = 0.5; —···—SP = 1.0 m/day.

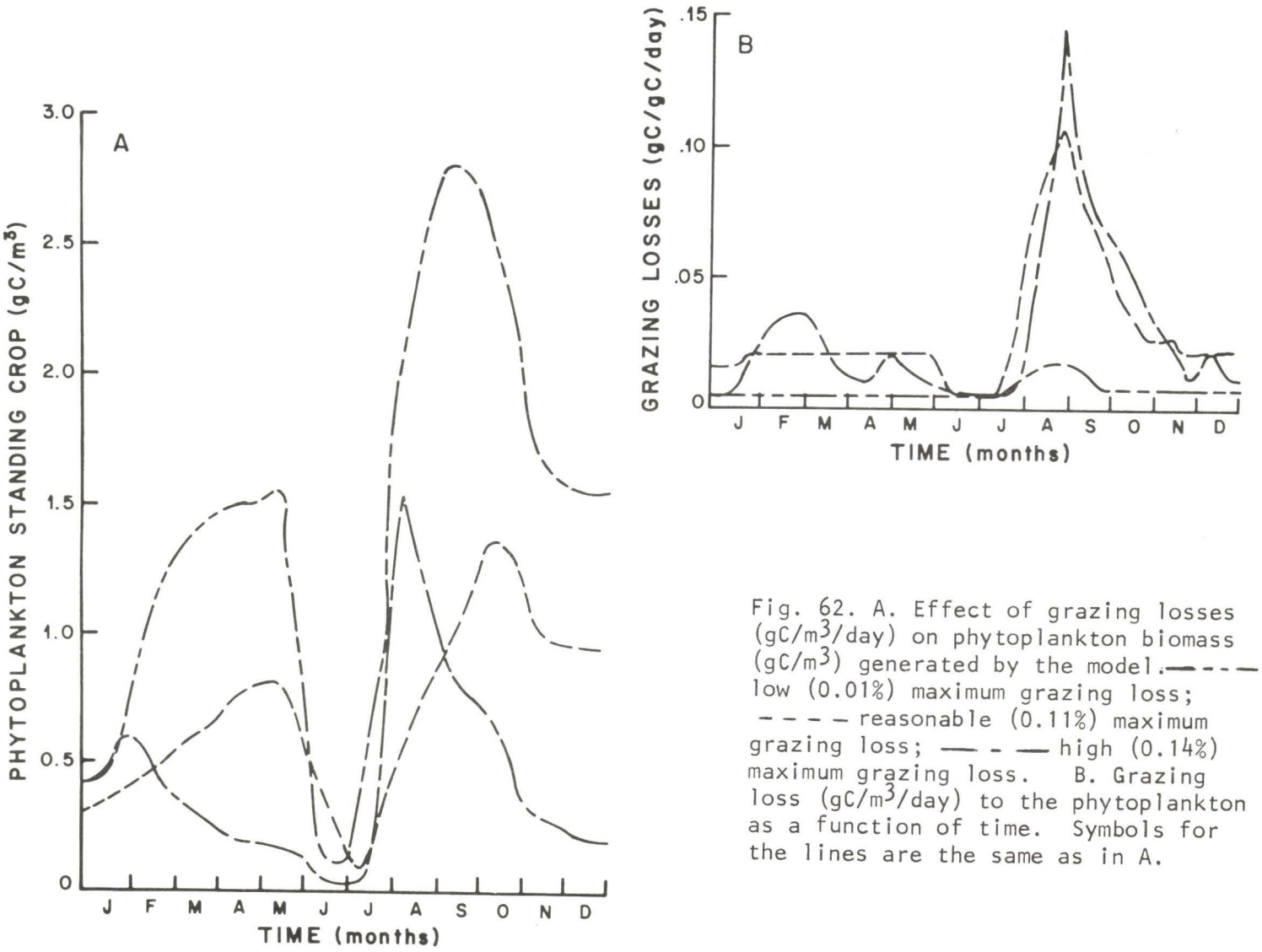

Fig. 62. A. Effect of grazing losses (gC/m^3/day) on phytoplankton biomass (gC/m^3) generated by the model. — — — low (0.01%) maximum grazing loss; — — — reasonable (0.11%) maximum grazing loss; — - — high (0.14%) maximum grazing loss. B. Grazing loss (gC/m^3/day) to the phytoplankton as a function of time. Symbols for the lines are the same as in A.

TABLE 62. The effect of short circuiting on the phytoplankton. Output parameters considered are volume of the flushing channel (i.e., maximum volume flushed in one day), maximum flushing loss (gC/gC/day), magnitude and time of occurrence of fall and spring phytoplankton peaks, production rates, and standing crop at end of the year.

Output parameters	Volume of Short Circuiting Channel (m^3)						(no short circuiting)
	39,552	49,440	79,104	100,266	118,656	157,628	
A. Maximum flushing loss (gC/gC/day)	0.06	0.08	0.13	0.16	0.19	0.24	
B. Fall peak							
1. Standing crop (gC/m^3)	2.902	2.901	2.898	2.896	2.894	2.894	
2. Day of year	260	260	260	260	260	260	
C. Spring peak							
1. Standing crop (gC/m^3)	1.581	1.581	1.581	1.581	1.581	1.581	
2. Day of year	142	142	142	142	142	142	
D. Range of PSYN ($gC/m^3/day$)	0.028 to 0.405	0.028 to 0.405	0.024 to 0.403	0.016 to 0.397	0.011 to 0.399	0.009 to 0.399	
E. Range of production (gC/gC/day)	0.0556 to 0.2085	0.0556 to 0.2265	0.0556 to 0.2744	0.0556 to 0.2967	0.0556 to 0.3120	0.0556 to 0.3155	
F. Standing crop at year's end (gC/m^3)	1.60	1.60	1.60	1.60	1.60	1.60	
G. Minimum standing crop during year	0.52	0.39	0.17	0.09	0.06	0.05	

TABLE 63. The effects of changing sinking rates on the phytoplankton. Output parameters considered are the magnitude and time of occurrence of fall and spring phytoplankton peaks, production rates, and standing crop at the year's end.

Output parameters	Sinking rate (m/day)					
	0	0.25	0.50	0.75	1.0	4.0
A. Fall peak						
1. Standing crop (gC/m^3)	2.9	2.2	1.7	1.3	0.8	0.1
2. Day of year	260	257	255	257	267	267
B. Spring peak						
1. Standing crop (gC/m^3)	1.6	0.9	0.5	0.2	none	none
2. Day of year	142	142	142	142	none	none
C. Range of PSYN (gC/m^3/day)	0.009 to 0.399	0.004 to 0.353	0.002 to 0.292	0.000 to 0.229	0.000 to 0.155	0.000 to 0.028
D. Range of production (gC/gC/day)	0.0556 to 0.3155	0.0706 to 0.3538	0.0850 to 0.3933	0.0981 to 0.4084	0.1097 to 0.4428	0.1334 to 0.4585
E. Standing crop at year's end (gC/m^3)	1.6	1.0	0.5	0.3	0.1	0.0

TABLE 64. The effect of changing zooplanktonic grazing losses on the phytoplankton. Output parameters considered are magnitude and time of occurrence of fall and spring phytoplankton peaks, production rates, and standing crop at year's end.

Output parameters	Maximum grazing loss ($gC/m^3/day$)			
	0	0.014	0.114	0.142
A. Fall peak				
1. Standing crop (gC/m^3)	2.89	2.78	1.35	1.62
2. Day of year	260	262	261	229
B. Spring peak				
1. Standing crop (gC/m^3)	1.58	1.51	0.81	none
2. Day of year	142	142	142	none
C. Range of PSYN ($gC/m^3/day$)	0.009 to 0.399	0.008 to 0.390	0.002 to 0.195	0.000 to 0.337
D. Range of production (gC/gC/day)	0.0556 to 0.3155	0.0567 to 0.3223	0.0733 to 0.3825	0.1086 to 0.3985
E. Standing crop at year's end (gC/m^3)	1.60	1.54	0.93	0.16

to 1.6 gC/m^3. Various levels of grazing also had marked effects on the shape of the phytoplankton standing crop versus time curve (Fig. 62). An increase in grazing or sinking losses caused an increase in specific gross production rates, and a decrease in absolute gross production rates.

Model with all loss rates at reasonable levels

Reasonable loss rates were considered to be a sinking rate of 0.5 m/day, a respiration rate of 0.15 gC/gC/day at 15°C, flushing as occurred in 1972, and a maximum grazing rate of 0.08 gC/m^3/day. After deciding that these values represented reasonable rates, it was found that they were also in general agreement with values presented by Bannister (1974). A comparison of model output obtained with these parameters to model output obtained with only respiration and flushing losses is shown in Fig. 63. When all loss rates were in the model, the fall phytoplankton peak was lowered to approximately 17 percent of the level obtained with only flushing and respiration losses. The phytoplankton standing crop was always less than when only respiration and flushing losses were in the model. Finally, absolute gross production decreased, but specific gross production increased (see Table 57 "None (All reasonable)" column and Table 58 "PMAX = .075" and "RP = .15" column).

Effect of changing runoff parameters and loss rates with all loss rates at reasonable levels

The results of changing runoff parameters and loss rates on the simulation output for phytoplankton and zooplankton are shown in Table 56 and Table 57. The results are summarized in Table 65 and compared to the results of changing the same parameters with only respiration and flushing losses in the model. In general, the effects of changing a loss parameter (including runoff parameters) with all losses present in the model were the same as changing that parameter with only respiration and flushing losses in the model. For example, increasing RP, the respiration loss at 15°C, decreased

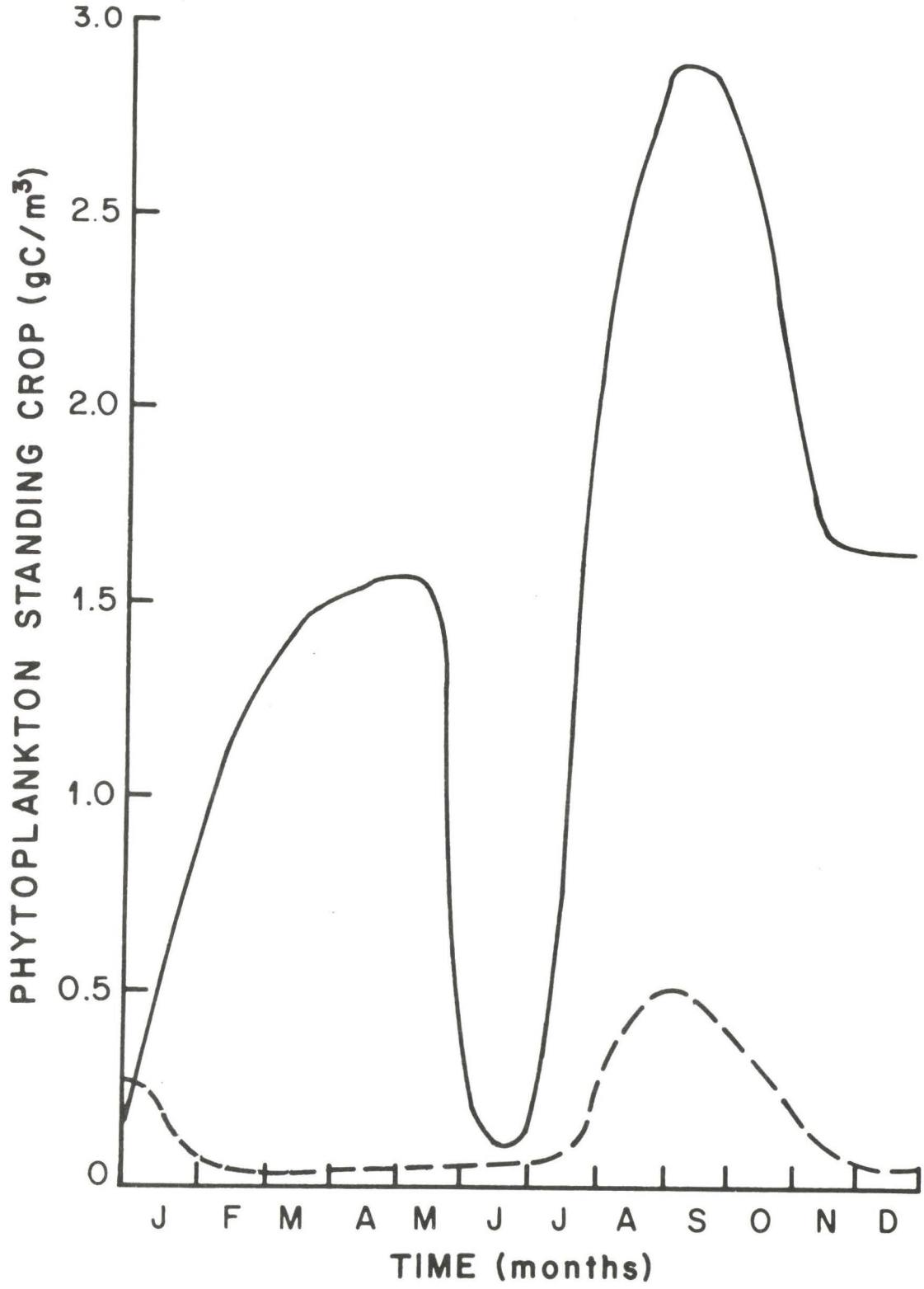

Fig. 63. Phytoplankton biomass (gC/m^3) generated by the model with reasonable loss rates: Comparison of output obtained with all losses in the model (— — —) with output obtained with only respiration and flushing losses in the model (———).

TABLE 65. Summary and comparison of the effects of changing losses and runoff parameters in the model with 1) all losses and 2) only respiration and flushing losses. As the losses in row one are increased, + means the phytoplankton or zooplankton parameter in column one increased or occurred later, - means the phytoplankton or zooplankton parameter decreased or occurred earlier, 0 means no change occurred, and C means a complex interaction occurred (usually a decrease in the parameter followed by an increase). RP+F indicates only respiration and flushing losses were present. "All" indicates all losses present; "N" indicates not evaluated.

	loss rates						runoff parameters						
	Respiration		Sinking		Grazing		Shape		Time		Magnitude		Short Circuiting
Output parameters	ALL	RP+F	ALL	RP+F	ALL	RP+F	ALL	RP+F	ALL	RP+F	ALL	RP+F	RP+F
A. Phytoplankton parameters													
1. Fall peak													
a. Standing crop	-	-	-	-	-	-	C	C	0	0	-	C	+
b. Day of year	-	-	+	C	-	-	C	C	+	+	C	+	0
2. Spring peak													
a. Standing crop	-	-	-	-	-	-	0	-	+	-	-	-	0
b. Day of year	0	-	0	-	0	-	0	-	+	-	0	-	0
3. Standing crop at year's end	-	-	-	-	-	-	C	0	+	0	-	0	0
4. PSYN ($gC/m^3/day$)	-	-	-	-	-	0	C	C	0	0	-	C	+
5. Production (gC/gC/day)	+	+	+	+	+	C	-	-	0	0	+	+	-
B. Zooplankton parameters													
1. Maximum standing crop	-	N	-	N	-	N	-	N	-	N	C	N	
2. Standing crop at year's end	-	N	-	N	-	N	0	N	+	N	+	N	
3. Maximum grazing	-	N	-	N	+	N	C	N	0	N	-	N	

the fall phytoplankton peak and the standing crop of phytoplankton at the end of the year, and shifted the day of the fall peak to earlier in the year. Increasing respiration also decreased absolute production and increased specific production. These changes occurred both when all losses were present in the model, and when only respiration and flushing were in the model.

However, with all losses included in the model interactions did occur that affected the response of the phytoplankton to changes in loss rates. For example, when grazing was increased in the presence of only respiration and flushing losses, specific production increased. However, if sinking losses were present, an increase in grazing losses caused an increase in the minimum specific production as previously, but a decrease in the maximum specific production (Table 57).

Discussion

All work with the model was completed prior to gathering data in the spring and summer of 1974. It was simply not possible to make any additional runs with the model which incorporated these most recent data.

Runoff parameters in nature and in the model

As discussed earlier, peak runoff may occur about 20 days later or 9 days earlier than in the comparison year, 1972. Thus shifts in the timing of runoff in the model to one month earlier or later represented radical changes that are not likely to occur in nature. A change of 15 days earlier or later in the time of occurrence of runoff is more likely to be representative of the changes that could be expected to occur in the Libby Lake watershed.

WRRI data suggest that a variation of 30 percent in the volume flow of runoff is likely to occur in Libby Creek and a variation of 50 percent is likely to occur for all streams in the Medicine Bow Mountains. Thus, for Libby Creek a variation of 50 percent is

likely to be greater than the variation that could be expected to occur in nature, and a variation of 100 percent represents a radical change that is not likely to occur.

During years of low runoff the model generated more runoff after the peak than actually occurred (see Fig. 43 and inset of Fig. 59). Therefore in the model the effects of flushing on the phytoplankton are greater than would occur in nature, and affect the phytoplankton for a longer period. Thus, in reality the effects of runoff during years of low volume flow should be even less than those predicted by the model.

Changing runoff parameters

Given that runoff occurs in the watershed, realistic shifts in the timing of runoff did not cause major effects on the phytoplankton. The phytoplankton standing crop at the year's end was always the same, so the phytoplankton as a whole appeared unaffected by long range or cumulative effects of the timing of runoff (Table 59, Fig. 57).

Increasing the total volume flow of runoff decreased the phytoplankton fall peak, and also the standing crop of phytoplankton at all times of the year. The general shape of the phytoplankton standing crop versus time curve was similar for all volume flows investigated. The phytoplankton survived changes even greater than those expected to occur in nature (Fig. 58, Table 60).

The data on runoff in the Snowy Range suggest that the shape of the runoff versus time curve in the Libby Lake watershed is a function of the total volume flow of runoff. Therefore, for Libby Lake it is not as important to know the shape of the runoff versus time curve as it is to know the magnitude of runoff. This would not be true for all lakes or reservoirs. Changing the shape of the runoff versus time curve decreased the effect of runoff. This occurred because the total volume flow of runoff was lowered, and hence the maximum flushing loss was decreased.

Short circuiting in effect lowers the total volume flow of runoff by setting an upper limit on the volume of the lake that can be flushed in one day. The effects of short circuiting occur only during the period of runoff. If short circuiting is occurring in Libby Lake, the maximum flushing loss to the phytoplankton would be set by a combination of both the degree of short circuiting and the absolute volume flow of runoff. As short circuiting becomes more important (i.e. as the volume of the rapidly flushing channel decreases), increases in the volume flow of runoff become less important in controlling the phytoplankton standing crop in the lake (Table 62). It is thus necessary to have data on short circuiting in Libby Lake before predicting the possible effects of weather modification.

The model predicts that changes in the temperature of runoff will not affect the phytoplankton standing crop or their production rates. This is probably due to two factors: 1) the volume flow of runoff is small in comparison to the volume of the lake during most of the year, and 2) the production rates appear to be influenced more by the amount of light available for photosynthesis than by temperature.

Weather modification and changes in runoff parameters

The timing of runoff does not appear to vary with the total volume flow of runoff (Rechard and Smith 1972, see also Fig. 43). Therefore, the timing of runoff is unlikely to be affected by increased snowpack. Also, since the time of occurrence of runoff varies naturally, the lake ecosystem has probably adapted to such variation. Thus, weather modification should not influence the lake via the timing of runoff.

The total volume flow of runoff, and with it the shape of the runoff versus time curve, is likely to be affected by weather modification. Weather modification should decrease the variation in the volume flow of runoff. However, even radical changes in the total volume flow of runoff did not have serious consequences for

phytoplankton in the model. Thus, even if weather modification did produce variations greater than 50 percent in the total volume flow of runoff, changes of this magnitude caused only slight changes in the magnitude of the phytoplankton's fall peak.

Weather modification might cause changes in the temperature of runoff waters, but the model predicts that even radical changes in runoff temperatures should have minor effects on both the phytoplankton standing crop and on the range of production.

Output of model with all losses compared to data from Libby Lake

When all loss rates in the model were at what was considered reasonable levels, the standing crop generated by the model was lower than actually occurred in the lake (Fig. 56). However, both standing crop versus time curves are of the same general shape. If sinking losses are removed from the model and grazing is at high levels (based on Haney's (1973) estimate for an oligotrophic lake of 6.6 percent of the phytoplankton standing crop per day), the standing crop curve generated by the model is in agreement with the data until about day 215 (August 2). Two possible explanations for this are: 1) sinking may not be an important factor in Libby Lake during the period from mid-July to mid-August, or 2) the PMAX values in the model were too low (i.e. the gross production rate was not high enough to allow for sinking losses). If PMAX was increased, the phytoplankton standing crop generated by the model was in good agreement with the data from Libby Lake until August (Fig. 56).

In all runs of the model with all losses, the difference between model output and the standing crop data from the field was greatest in late summer. This suggests that after day 215 (August 2), nutrients may be a major limiting factor. If nutrient limitation wre included in the model, the standing crop levels generated during August would be lower. Note however, that experience with the model suggests that the effects of runoff have the same pattern regardless of the absolute level of standing crop (Table 65).

Limiting factors

Dickman (1969) has categorized factors that limit absolute production as cropping factors such as flushing, grazing and sinking, and resource factors such as nutrients, temperature and light. Cropping factors limit absolute production by removing individuals from the population and therefore decrease the standing crop. Resource factors limit production by limiting specific growth rates. Bannister (1974) has categorized factors that limit standing crop and production as dynamic and "other," Dynamic limits are set by the balance between production and loss rates, and vary with time.

The model output suggests that different factors limit the phytoplankton standing crop at different times of the year. It appears that light and temperature are the major limiting factors during winter, sinking and grazing during the early spring (if sinking is not counteracted in Libby by mixing due to wind), flushing during spring runoff, grazing after runoff, and nutrients at the end of the summer.

The model suggests that in general cropping factors control the magnitude of the phytoplankton standing crop (Figs. 58, 61, 62). Since cropping factors appear to be at reasonable levels in the model, the disagreement between the generated standing crops and the data is probably due to resource factors. Light and temperature in the model mimic field data. Nutrients are the only major resource factor not considered in the model. Assuming that the processes and equations associated with light and temperature are correct, nutrient limitation may then be the source of disagreement between the standing crop generated by the model and the data from Libby Lake.

According to a dynamic theory of limitation, the source of disagreement between the model and the data in regard to standing crop is the balance between production rates and loss rates. The effects of grazing losses on the phytoplankton standing crop show the complex nature of this balance (Fig. 62, Table 64). As grazing losses increase specific gross production increases. But as grazing losses increase, the standing crop of phytoplankton and the absolute

gross production rates decrease and then increase. Grazing then, which is a cropping factor, sets a dynamic limit on the phytoplankton standing crop and production.

In general, the model generated absolute gross production rates that were high, and specific gross production rates that were low in comparison to other oligotrophic lakes. The disagreement in production rates on a m^3 or a m^2 basis is not disturbing because of the probability of large variation in the standing crop associated with the values in the literature. The differences between the model and the literature would probably decrease if actual loss rates in Libby Lake were known and the effects of nutrient limitation were considered. Experience with the model, and Bannister's (1974) discussion of dynamic limiting factors, suggest that it would be possible to select parameters that would limit production to the range found in the literature. However, with the lack of data on rates of production from Libby Lake, this was not considered worthwhile at the present time.

The small amount of productivity data that are available from Libby Lake agreed well with Wagner's (1971) data from Little Brooklyn Lake. However, with all loss rates in the model it was impossible to generate both phytoplankton standing crop levels that agreed with Libby Lake data, and specific production rates that agreed with Wagner's data. Again, the disagreement is probably due to the facts that nutrients are not considered in the model, and that production rates are the result of a dynamic balanace between standing crop, production and losses.

This study emphasized the possible effects of weather modification, via runoff, on the phytoplnakton during the ice free period. Weather modification might, however, have serious consequences for the phytoplankton during the winter. The critical factor for the phytoplankton during the winter is probably light. An increased snow cover on the lake during winter might well reduce the light levels enough to allow anerobic conditions under the ice (Wright 1964). This is not likely to occur at Libby, since the depth of snow on the

lake is probably determined by the wind and not by the absolute amount of snowfall. This study predicts that in summer the effects of weather modification on the phytoplankton of Libby Lake would be minimal and not of serious consequence for the ecosystem as a whole. However, there is simply not enough known about the winter ecology of high mountain lakes to predict the possible effects of weather modification on the lake during the winter.

Summary of model output

Assuming that the parameters and equations in the model are valid, the model predicts that a change in the timing of runoff causes an equal change in the timing of the phytoplankton spring and fall peaks, but does not change the magnitude of the phytoplankton standing crop. Changes in the magnitude of runoff are inversely related to changes in the magnitude of the phytoplankton standing crop. Changing the shape of the runoff versus time curve, which also changes the magnitude of runoff, leads to a slight increase in the fall phytoplankton peak and tends to spread the effects of runoff over a longer time. In general, changing the shape of the runoff versus time curve from very peaked to broad decreases the effect of runoff on the phytoplankton.

The effect of runoff on the phytoplankton can be modified by short circuiting. The more short circuiting that occurs, the less effect runoff has on the phytoplankton.

Effects of runoff on water temperature are not likely to be important in Libby Lake.

In all cases increased losses to the phytoplankton caused by increasing respiration rate, sinking rate or grazing rate led to decreased phytoplankton standing crop and absolute gross production, and increased specific gross production. The effects of changing runoff parameters with all losses in the model (i.e. flushing, respiration, sinking and grazing) were generally the same as when only respiration and flushing losses were included.

The proposed weather modification program would affect only the total volume flow of runoff and the shape of the runoff versus time curve. The model predicts that even radical changes in these runoff parameters do not have serious consequence for the phytoplankton. It is unlikely, then, that changes in runoff parameters caused by weather modification will have serious consequences for the phytoplankton.

Model output in relation to field work

The equation for PMAX used in the model (eq. 3) generates more or less reasonable values at cooler temperatures, but underestimates PMAX considerably at warm temperatures (Fig. 52B dashed line). The data appear to fit an exponential relation between PMAX and temperature better than a linear relation. Alternatively it may be that the data are discontinuous, and that ice-covered and ice-free periods should be treated separately. With the limited data available it is not possible to determine which alternative is closest to what actually occurs.

The equations used to calculate XKP in the model also do not give values agreeing with observed values at all times of the year. The model's values are reasonable only during the time near ice break up. The following table compares observed values of XKP with those used in the model.

Time of Year	Model's XKP	Observed XKP
17-XI to 21-V	.05	.01
22-V to 20-VI	.07	.015 - .05
21-VI to 17-X	.09	.05 - .13
18-X to 16-XI	.07	(.03 - .01)

When the average production m^{-3} (PSYN, eq. 2) is calculated based on actually observed standing crops, the model predicts

accurately for times of ice cover, gives values about 40 percent low at the time of ice break up, and is within about 15 to 20 percent of observed values during the rest of the summer (Fig. 50 non-hatched bars; the observed value for VIII-1-74 is somewhat low as there was intermittent cloud cover toward the end of the incubation). Predicted values of 15 to 20 percent of observed values seem very reasonable. When the same calculations are made using the measured values of PMAX and XKP instead of those programmed in the model, the predicted average production m^{-3} is much greater (175 percent greater) in mid-summer than that actually observed (Fig. 50 hatched bars), probably because the model assumes a homogeneous vertical distribution of algae. When large standing crops build up at lower depths, use of the average standing crop m^{-3} in equation 2 overestimates the algae in the upper layers where there is more light for photosynthesis. This in turn leads to the overestimate of mg C m^{-3} day^{-1}.

The model, therefore, produces more or less reasonable estimates of specific production, but it gives a "correct" answer for the wrong reasons. During winter the model calculates more light penetrating the ice than actually occurs, but this overestimate is balanced by the model's underestimate of how "efficiently" the algae can utilize the light available. During the ice free period the model's values of PMAX and XKP are low, but this error is compensated for by larger apparent average standing crops m^{-3} in the upper lighted layers than actually occurred. The latter is again owing to the build up of large phytoplankton standing crops below the epilimnion.

Thus, GIVEN that the standing crop in the model is that which occurs in the lake at any time, the model will predict the average rate of production m^{-3} fairly accurately. If the standing crop "provided" for the model is incorrect, the value of standing crop (SC in eq. 2) will be higher or lower than actually occurred, and the estimate of average production m^{-3} will be correspondingly higher or lower than actually occurred.

In the model the algal standing crop is a function of the difference between rate of input (photosynthesis) and rates of loss

(respiration, flushing, grazing, sinking). Assume that at a given point in time the model's estimates of losses are low relative to gains, but that the model's estimate of standing crop is correct. Then although the model predicts the average production m^{-3} accurately initially, losses are low, and the standing crop of algae will build up to unreasonably large values despite accurate estimates of specific production. The increasing standing crops then lead to ever increasing overestimates of average production m^{-3}, which lead to increased standing crop, and so on. In runs with the model, this phenomenon occurred after mid-summer.

The model predicts increased specific productivity at higher loss rates. This is verified by the data on birth rate index (BRI) for the flushing layer of the lake (e.g. Fig. 53). This effect is expected because of the relation between standing crop and available light. As algal standing crop increases, the extinction of light increases sine the algae absorb light. At high flushing rates (low retention time) algal standing crop is low, there is more light and specific production (i.e. BRI) is higher.

The three variables of flushing, grazing and solar radiation can account for almost all the variation observed in the BRI at a significance level of less than 0.05. The two variables of flushing and grazing (both losses) can account for about 94 percent of the variation in the death rate index (DRI), but only at the 0.1 level of significance. If sinking, another potentially important loss, were taken into account, the DRI F statistic probably would become highly significant. From these data we conclude that cropping factors almost always must be more important than resource factors in controlling algal standing crop in the lake. Additional effort could best be put into refining estimates of loss rate (cropping) relationships rather than nutrient limitation (resource) relationships.

In runs with the model, the difference between output and field data on algal standing crop was greatest after mid to late summer. During this time the predicted algal standing crop is higher than observed. The reasons for this discrepancy appear to be largely

1) the model overestimates production rates in the fall, and
2) grazing is probably more intense than we had thought it would be. About the time runoff ends, the standing crop of Daphnia pulex builds up to very high levels which probably extend into October (Fig. 45). The overestimate of gains (photosynthesis) and the underestimate of losses combine to allow the larger-than-observed algal standing crop.

Prior to mid-summer the model's predictions about algal standing crop appear fairly reasonable in a quantitative sense. Overall, the model's predictions can be considered as fairly reasonable only in a qualitative or semiquantitative sense. That is, changes in the general pattern or shape of the algal standing crop versus time curve as a function of, say, changing runoff parameters are probably reasonable. The predicted absolute values of standing crop through the whole year obviously are inaccurate.

Planktonic algae often comprise a large portion of the food available for benthic herbivores in lakes. If this is true in Libby Lake, over a long period of years the intermittent additional 10 to 15 percent of runoff from weather modification could decrease the amount of food for the herbivorous benthos and zooplankton. This in turn could affect the lake's fishery. Note, however, that algae flushed from the lake become available as food for benthic herbivores in Libby Creek. Alternatively, the effect of weather modification's decreasing the contribution of phytoplankton as food for the lake's benthic herbivores could be offset by increased perlphytic production. There are no data available to evaluate these partially conflicting possibilities, but the possibilities do exist.

Conclusions

1) The model predicts average phytoplankton specific production fairly accurately, but for the incorrect reasons. However, the qualitative or semiquantitative predictions of the model about the phytoplankton community are still considered as being reasonably trustworthy.

2) A combination of volume flow and depth of mixing layer yielding a retention time of seven to ten days or less will lead to decreases in algal standing crop in the flushing layer. Since this will certainly occur every spring, runoff will always strongly influence the phytoplankton standing crop.
3) For any given total volume of runoff, a prolonged period of runoff (a cool as opposed to warm spring) will extend the influence of flushing through time. The greater the total volume of runoff, the greater the effect of flushing on the lake's phytoplankton community.
4) Given that weather modification will increase the total snowpack, and hence total runoff, only by about 10 to 15 percent in years of less than maximum snowpack, the lake will not suffer any perturbation which would not occur in the absence of weather modification. The additional 10 to 15 percent of runoff will decrease phytoplankton standing crop to levels below those which would occur in the absence of weather modification. The amount of this reduction in standing crop will depend on a variety of factors not influenced by winter weather modification (e.g. spring air temperatures, depth of epilimnion as influenced by wind).

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SILVER IODIDE: ITS MOVEMENT IN AN ALPINE ECOSYSTEM AND ITS EFFECT ON TWO PLANT SPECIES

P. Singleton and R. White

At the present time silver iodide is the primary nucleating agent used for weather modification projects. It is quite reasonable to assume that the concentrations of silver (Ag) and silver compounds in the Medicine Bow Mountains will increase if a cloud seeding program is continued for a period of many years. Existing information suggests that the right conditions for cloud seeding, assuming the proper use of existing technology, may occur 40 to 50 days per winter in the Medicine Bow Mountains (Don Veal, personal communication).

Because water is such a limiting factor over much of the western Great Plains, farmers and ranchers may become dependent on whatever additional water can be produced by seeding with AgI, and thus there is the potential of having AgI added to the environment every winter for a long period of time. Although the annual rate of AgI addition may be low, it is possible that toxic levels will accumulate. Research has shown that Ag can be very toxic to some organisms, therefore we initiated a research program to determine 1) the natural concentrations of Ag in various components of the Medicine Bow ecosystems, 2) the movement of the relatively insoluble AgI through the soil, 3) the uptake and accumulation of Ag by two plant speices, and 4) the sensitivity of two plant species to various concentrations of Ag or Ag compounds. The results of these studies are reported below with the exception of natural Ag concentrations which were reported earlier (beginning on page 10).

Silver Iodide

Douglas (1968) lists the following characteristics for AgI:

- Pale yellow powder, hexagonal structure
- Molecular weight 234.8 (46 percent Ag and 54 percent I)
- Melting point 556°C, with some decomposition at 552°C
- Boiling point 1506°C
- Density 5.675 gm/cc
- Vapor pressure 1 mm at 820°C
- Solubility 3×10^{-7} gm/100 ml cold water

AgI is one of the least water-soluble compounds.

As early as 1899 the toxic effects of silver were being explored. Clark (1899) found that silver nitrate and mercuric chloride were equally toxic to molds, followed by potassium dichromate and foramldehyde. Just and Szniolis (1936) found that aquatic fauna were extremely sensitive to the presence of small quantities of silver in water and that comparatively small doses of silver caused poisoning and death.

Douglas (1968) reports that current weather modification techniques supply on the order of 10^3 to 10^4 AgI particles per cubic meter to the atmosphere over the target area. This is 1×10^{-5} to 1×10^{-4} of the maximum permissible airborne concentration for occupational exposure of soluble silver compounds. Douglas, however, warned that the concentration near ground generators exceeds the maximum concentration of airborne particles of 10^4 particles per cubic meter and could be hazardous because of the iodide vapor. Woodward (1963) stated that the USPH drinking water standard of 50 ppb is not based on toxicity, but is used to prevent Argyria, a cosmetically objectionable disease that can be caused from prolonged consumption of silver.

Cooper and Jolly (1960) do not feel that iodine poses any environmental problems. On the other hand they state, "Silver is a paradoxical substance; widely used in industry, because of its great potency as a microbial poison, it is relatively harmless to higher animals including man."

Amounts of silver iodide used in precipitation management vary depending on the type of management. Cooper and Jolly (1960) list values from 6 to 100,000 grams AgI per hour depending on the kind of generator used and the type of management project. One generator is generally used for every 100 square miles of target area.

Silver concentrations in precipitation from seeded storms range from 0.00001 to 0.00176 ppm, and concentrations in non-seeded storms have been measured at levels up to 0.00002 ppm (Cooper and Jolly 1960). Precipitation from seeded clouds could add 0.01 to 0.03 grams of silver per hectare per centimeter of rain (Cooper and Jolly 1960). The average natural Ag concentration in the soils of the Medicine Bow Mountains is about 0.06 ppm, which is equal to approximately 136 gms Ag/hectare-15 cm of soil. If the normal precipitation is increased by 20 percent each year, for example from 75 to 90 cm, the yearly addition of Ag from seeded clouds would amount to 0.3 gms/hectare (assuming .02 gm Ag added per cm of precipitation). Assuming these figures are reasonable, it would take approximately 453 years (136 ÷ 0.3) cloud seeding to double the natural Ag concentration.

Silver iodide is burned in ground based generators with sodium iodide and acetone. Potassium iodide has been used to some extent in place of sodium iodide. Although considerable work has been done to determine the nature of the aerosol produced from generators, and consequently the mixture that contacts the ground, no definite conclusions have been drawn.

dePenta and Caimi (1967), working with a silver iodide-potassium iodide mixture, deduced from chemical analysis that the aerosol is composed of silver and iodide in the ratio of approximately 2:1. They conclude that because all particles are surrounded by replicas of drops showing a homogeneous hygroscopic feature, the aerosol is not a mixture of both salts. They write, "It may be a double salt or a solid solution of silver and potassium iodide or a combination thereof." Whatever it is, they are certain it is a hygroscopic

compound, at least at the saturation point, and that drops formed contain suspended silver iodide.

Mossop and Tuck-Lee (1968), Mason and Hallet (1956), Edwards and Evans (1960), and Davis (1969) have all investigated the nature of ignition products produced from burning silver iodide and sodium iodide in generators. The general conclusion is that the ignition product which reaches the ground is likely to be a solid, hygroscopic compound, composed of AgI-NaI complexes with unknown solubility and ionization potential.

Koenig (1964), studying the aerosols produced by several devices used to provide silver iodide for cloud seeding, found that particles produced by different types of silver iodide generators varied in their chemical and physical properties. He was unable to determine the mixtures that would actually reach the ground.

Silver Movement on Libby Flats

Very little work has been done regarding the movement of silver in soils and plants. Preliminary work indicates that silver will not move great distances in soils. Teller and Cameron (1972) have concluded from working with soil cores that the largest accumulation of silver from infiltrating solutions takes place in the litter and surface two centimeters of soil, and that this accumulation ranges from 60 to 99 percent of the Ag added to the surface.

In August of 1972 a study was initiated in a subalpine meadow on Libby Flats (3210 m) (near site 20, page 11) to determine the degree and rate of silver movement through the soil profile as a result of leaching by natural precipitation. The study was also designed to indicate if the Ag content of plants could be influenced by the silver content of the soil. The design of the study is a latin square consisting of 16 nine-square-meter plots (fig. 64). Four silver treatments were used, consisting of 1) a control containing 0.06 ppm natural silver content in the soil, 2) 0.12 ppm Ag, 3) 0.24 ppm Ag, and 4) 0.48 ppm Ag. Silver iodide applications were

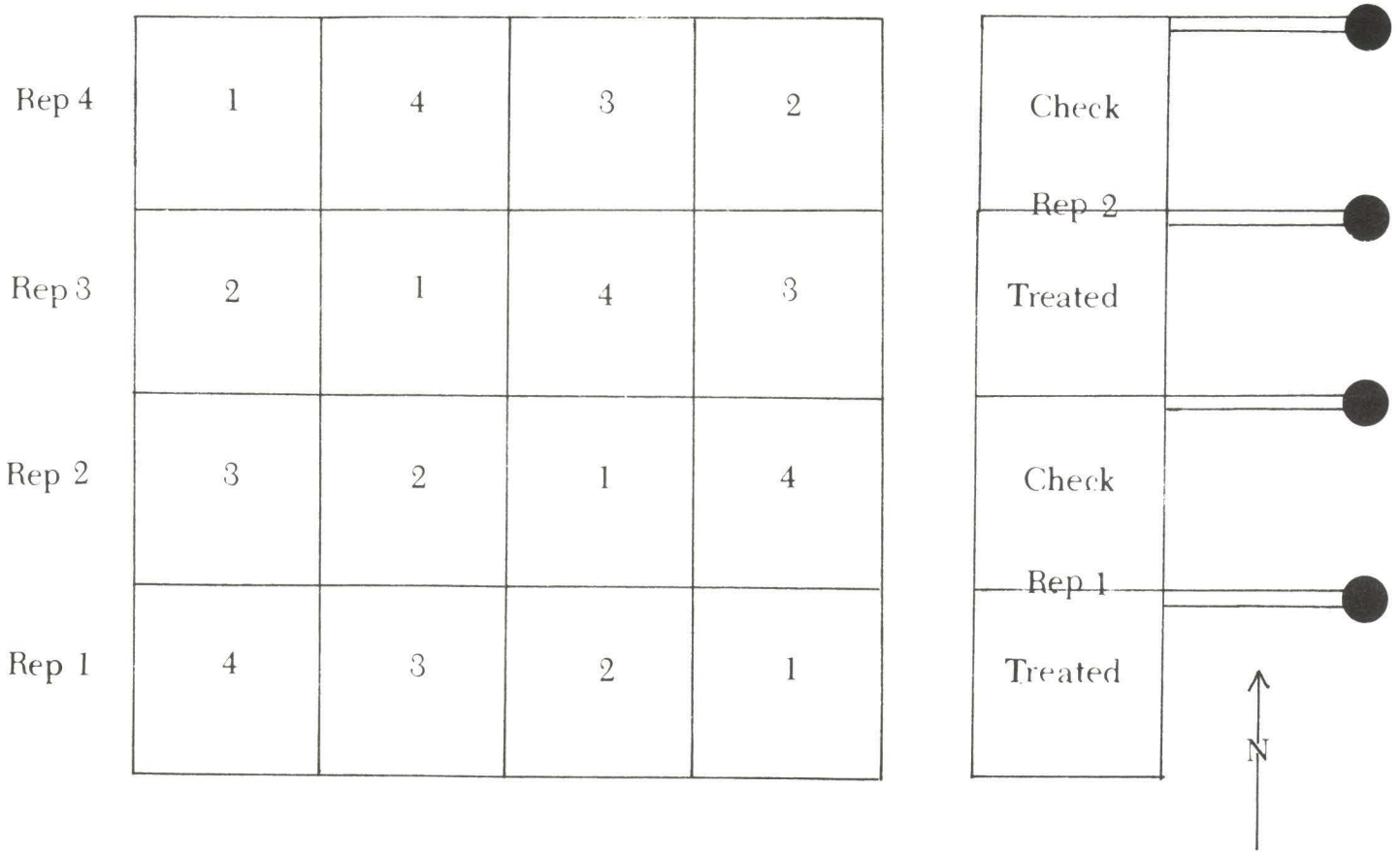

Fig. 64. Experimental design for the Libby Flats silver movement study. The runoff plots (on the right) were contaminated at eight times natural silver in the soil; runoff water was collected in sunken containers downslope from the plots and analyzed for silver concentration. The 16 plots on the left were treated as follows: 1 - controls (0.06 ppm natural Ag in soil), 2 - double natural Ag in soil (approx. 0.12 ppm), 3 - four times natural Ag in soil (approx. 0.24 ppm), 4 - eight times natural Ag in soil (approx. 0.48 ppm). Each plot is 9 m^2.

calculated to raise the Ag content to the above levels in the top 15 cm of soil.

After a year of natural precipitation, soil samples were taken at four depths in each of the plots 0-2.5 cm, 2.5-5 cm, 5-7.7 cm and 7.5-10 cm. The samples were than analyzed for Ag at the lab mentioned on page 12. Composite samples of the forbs and grasses were collected separately at each plot from 3 randomly placed quadrats (.33 m^2). These composite samples also were submitted for Ag analysis.

Another study adjacent to the above plots was initiated to determine if the Ag content of runoff water is influenced by the silver content of the soil (Fig. 64). This study consisted of two treatments: 1) a control containing 0.06 ppm Ag in the soil, and 2) 0.48 ppm Ag in the soil, replicated two times.

Plots for both of the above studies were constructed of 10 cm galvanized lawn edging. The lawn edging was buried 5 cm in the soil to prevent lateral movement of Ag from one plot to another. For the runoff studies, pipe was installed connecting each plot to a buried container which caught the runoff water. Water collected in the spring runoff of 1973 was analyzed for Ag.

A solution of 0.25 percent AgI and 0.08 percent NH_4I (by weight) in acetone was used to contaminate the plots in the above studies. Acetone is required to keep AgI in solution. Aliquots of the solution, diluted with eight liters of H_2O, were applied. An equivalent amount of acetone was added to all plots including the control. After application of the solution the plots were sprayed with water to prevent any burning of the vegetation that may have occurred from the application of acetone.

Results and Discussion

Vegetation. Table 66 shows the Ag concentration in the forbs and grass for the four treatments. Both vegetation types accumulated significantly more silver under the two high treatments.

Table 66. Comparison of means for accumulation of silver in forbs and grasses on plots located on Libby Flats. Figures labeled with the same letter in each column are not significantly different at .05 level. Figures are given in ppm dry matter.

Treatment	Forbs	Grasses
Check	0.019 a	0.042 a
0.12 ppm Ag	0.330 a	0.270 a
0.24 ppm Ag	5.023 b	7.032 b
0.48 ppm Ag	7.103 b	7.205 b

In both forbs and grasses there was a big increase in Ag accumulation between the 0.12 ppm treatment and the 0.24 ppm Ag treatment. Although the 0.24 ppm treatment is only twice as great as the 0.12 ppm Ag treatment, the difference in accumulated silver is more than 15 times greater in forbs and 26 times greater in grasses. In contrast, the jump between 0.24 ppm Ag and 0.48 ppm Ag was slight.

From these data, it appears that plants will accumulate large amounts of Ag when the Ag content of the soil is at some point between 0.12 and 0.24 ppm. After 0.24 ppm and up to 0.48 ppm silver, there is very little additional accumulation of silver by the plants.

A nominal difference can be the amount of silver accumulated under the four treatments. In comparing the two, grass accumulated significantly more silver under natural conditions. This was the only significant difference found between the two types.

Soil. Fig. 65 illustrates the movement of silver through the soil under the four treatments. It is evident from the graph that most of the silver applied to the plots remained in the top 2.5 cm of soil.

The natural silver present in the soil varied little with depth; no significant differences were found between the four depths at the

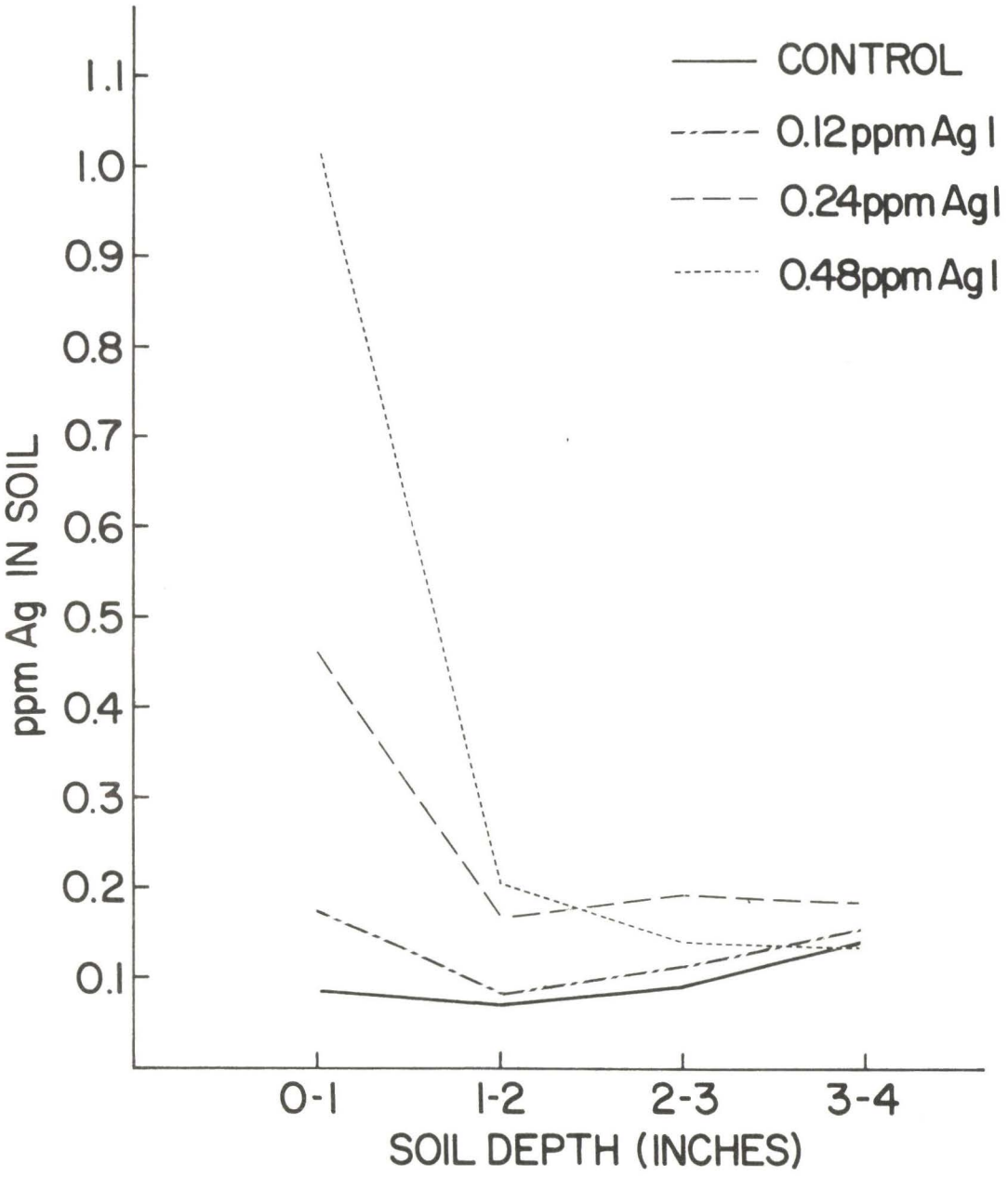

Fig. 65. The concentration of Ag at various depths in the soil, one year after application.

0.5 level of significance (Table 67). Natural silver shows a low point in the 2.5-5 cm depth with increasing silver both above and below this depth. It appears that natural silver is leached or depleted from the 2.5-5 cm depth. The possibility exists that Ag uptake by plants reduces the Ag content in this zone of the soil profile. Alternately, assuming a natural increase in Ag content of soil with depth, one can postulate that the silver levels in the 0-2.5 cm zone are higher than in the 2.5-5 cm depth because of silver deposited near the surface by decomposing plants. The plants accumulate the silver from deeper soil zones, and subsequently silver is deposited in the top layer through the decomposition of organic matter.

Table 67. Comparison of mean Ag concentration within treatments at the four different depths. Means not labeled with same letters in each column are significantly different at .05 level of significance. Each figure is the average of four observations.

Depths	Control	0.12 ppm Ag	0.24 ppm Ag	0.48 ppm Ag
0-2.5 cm	.092 a	.171 a	.479 a	1.018 a
2.5-5 cm	.070 a	.102 a	.164 b	.193 b
5-7.5 cm	.096 a	.120 a	.171 b	.133 b
7.5-10 cm	.106 a	.125 a	.150 b	.106 b

Silver was present at higher concentrations in the upper 2.5 cm of the soil profile in all of the treatments, although the 0.12 ppm treatment was not statistically significant (.05 level). It is interesting to note that in both the 0.12 and 0.24 ppm treatments there was a trend similar to the control. Ag levels were lower in the 2.5-5.0 cm zone than in the soil layers both above and below this depth. This may have been caused by the natural cycling process suggested earlier.

In the 0.12 and 0.24 ppm treatments most of the silver stayed in the 0-2.5 cm level, although both treatments were somewhat higher than the control at the three other depths.

In the 0.48 ppm treatment, as was evident in the two lesser treatments, most of the silver was accumulated in the top 2.5 cm of soil. It is interesting to note that the 0.48 ppm treatment was the same as the control at the 7.5-10 cm depth and lower than both the 0.12 ppm and 0.24 ppm silver treatments (Fig. 65). It appears that under the 0.48 ppm Ag treatment the silver was more tightly held in the soil in the top two levels (0-2.5 cm and 2.5-5 cm), and thus did not leach into the lower levels. This could be related to interactions between the Ag applied and soil microorganisms.

Table 67 illustrates that there were very few significant differences between treatments at different depths. In Table 67 one can see that the 0-2.5 cm depth was significantly greater than the three other depths in the 0.24 and 0.48 ppm Ag treatments. All other depths revealed no significant differences within each treatment.

It appears that the lower Ag applications were leached farther into the soil than the heavy application. The light applications follow a trend very similar to the control, but they are higher in the amounts of silver at all four depths.

Runoff Studies. Table 68 shows the values obtained from the runoff studies. Runoff water from the treated area contained almost eight times as much silver as runoff water from the control. This corresponds closely with the treatments; the control treatment contained 0.06 ppm silver while the treated area contained 0.48 ppm silver, also an eight fold difference. However, because of the variability between replications, no definite relationship can be drawn between the amount of Ag in runoff water and that contained in the soil. Perhaps the data do show a trend.

Table 68. Values of Ag concentration (ppm) obtained from runoff studies conducted on Libby Flats.

	Check	Treated
Rep I	1.1×10^{-5}	1.8×10^{-3}
Rep II	9.0×10^{-4}	5.0×10^{-3}
Mean	4.6×10^{-4}	3.4×10^{-3}

It is possible that silver iodide applied through cloud seeding operations would not react in the same manner as the silver iodide applied to the study plots.

The Effect of Silver Iodide on the Germination and Development of Two Plant Species

A greenhouse study was conducted to determine the influence of Ag on percentage emergence and seedling development of two common plant species of the Medicine Bow Mountains, tufted hairgrass (Deschampsia caespitosa) and lodgepole pine (Pinus contorta). The pine seeds were purchased from a commercial seed company, and tufted hairgrass seeds were collected from the study area during the fall of 1972.

Soil for this study was collected from under grass and lodgepole forest communities on the study area. The lodgepole soil was a clay loam, pH 5.0; the grass soil was a sandy clay loam, pH 5.8. The soil was first screened through a 6.3 mm mesh screen to remove large rocks and roots, and then placed in pint cartons. The soil added to each carton was weighed to insure constant concentrations of silver when the solution of Ag was added to the soil.

Both the grass and tree species were tested using a completely randomized design with four treatments and 15 replications, giving a total of 60 pots for each experiment. After the addition of soil to the pots, a mixture of 0.25 percent AgI and 0.08 percent NH_4I by weight in acetone was applied to give the desired concentration for

each treatment.[1] Treatments were 1) control with only natural Ag in acetone and the soil, approximately 0.06 ppm; 2) 10 times natural or approximately 0.6 ppm; 3) 100 times natural or approximately 6.0 ppm; and 4) 1,000 times natural or approximately 60 ppm. Four days after treatment 50 seeds of lodgepole pine or 50 seeds of tufted hairgrass were planted in each pot, depending upon the experiment. The grasses were grown for two months and the lodgepole pine was grown for four months. Emergence counts were made at intervals of two days for the grasses and one week for the pine. At the end of the growth period the plants were harvested and above- and below-ground production were determined on a dry weight basis. Plant parts were dried for 24 hours at 70°C. To determine the amounts of silver taken up by the two species, foliage from five pots for each treatment was combined to give sufficient plant material for analysis, thereby providing three replications for each of the four treatments. The Ag concentrations were determined as described on page 12.

A germination experiment was also conducted, using a 1.5 percent agar substrate as a germinating medium. Silver iodide, in a solution of NH_4I and acetone, was added to the agar while in a liquid state. The mixture was then autoclaved and poured into sterile petri dishes.

Experiments with both species were conducted using a randomized complete block design with four replications of each treatment and 50 seeds per sample. Four treatments were used in the two experiments, 1) a control, 2) 10 ppm, 3) 100 ppm, and 4) 1,000 ppm AgI. Similar seeds were used as mentioned previously for the plant development study. Germination was recorded daily for 2.5 months for the tree seeds; seeds were considered germinated only when the length of the radical exceeded that of the seed. The tufted hairgrass seeds were germinated in a chamber programmed to maintain temperature for 12 hours at 30°C and 12 hours at 20°C, while the pine seeds were germinated at a constant 30°C.

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[1] NH_4I is necessary to bring the highly insoluble AgI into solution, and is used in nuclei generators.

Results and Discussion

Fig. 66A shows the percentage of emergence and Fig. 66B the percentage germination for tufted hairgrass subjected to different AgI concentrations. The average emergence of the four treatments after 32 days was 26.2 percent, while the average germination after 23 days was 39.2 percent. It is evident that silver iodide has a greater effect on percentage emergence than on percentage germination of tufted hairgrass seed. Although lower levels of AgI were used for the emergence trials than for the germination trials, the toxic effect was most evident on emergence. Sixty ppm AgI significantly decreased emergence, while no statistically significant difference (.05 level) was found between the four treatments in the germination study, although the 1,000 ppm AgI treatment had a tendency to inhibit germination.

The 6.0 ppm and 100 ppm AgI treatments increased both percentage of emergence and germination, although the increases were not statistically significant (.05 level). Klein and Sokol (1973), while studying generator sites, found that increased amounts of Ag in the soil were correlated with increased respiration of microbial populations.

The difference between percentage emergence and percentage germination of pine was not as great as for tufted hairgrass (Fig. 67). The mean of the four treatments 93 days after planting for percentage emergence was 27.9 percent. The mean for percentage germination 80 days after planting was 32.4 percent. The 60 ppm AgI treatment significantly reduced seedling emergence in lodgepole pine 93 days after planting, while the 0.6 ppm AgI treatment significantly increased emergence over the other three treatments. As was observed with grass, the four AgI treatments yielded no significant difference in the percentage germination of lodgepole pine.

Effects of AgI on percentage germination were very minute for both tufted hairgrass and lodgepole pine. No significant differences were found between the four treatments, even though these treatments

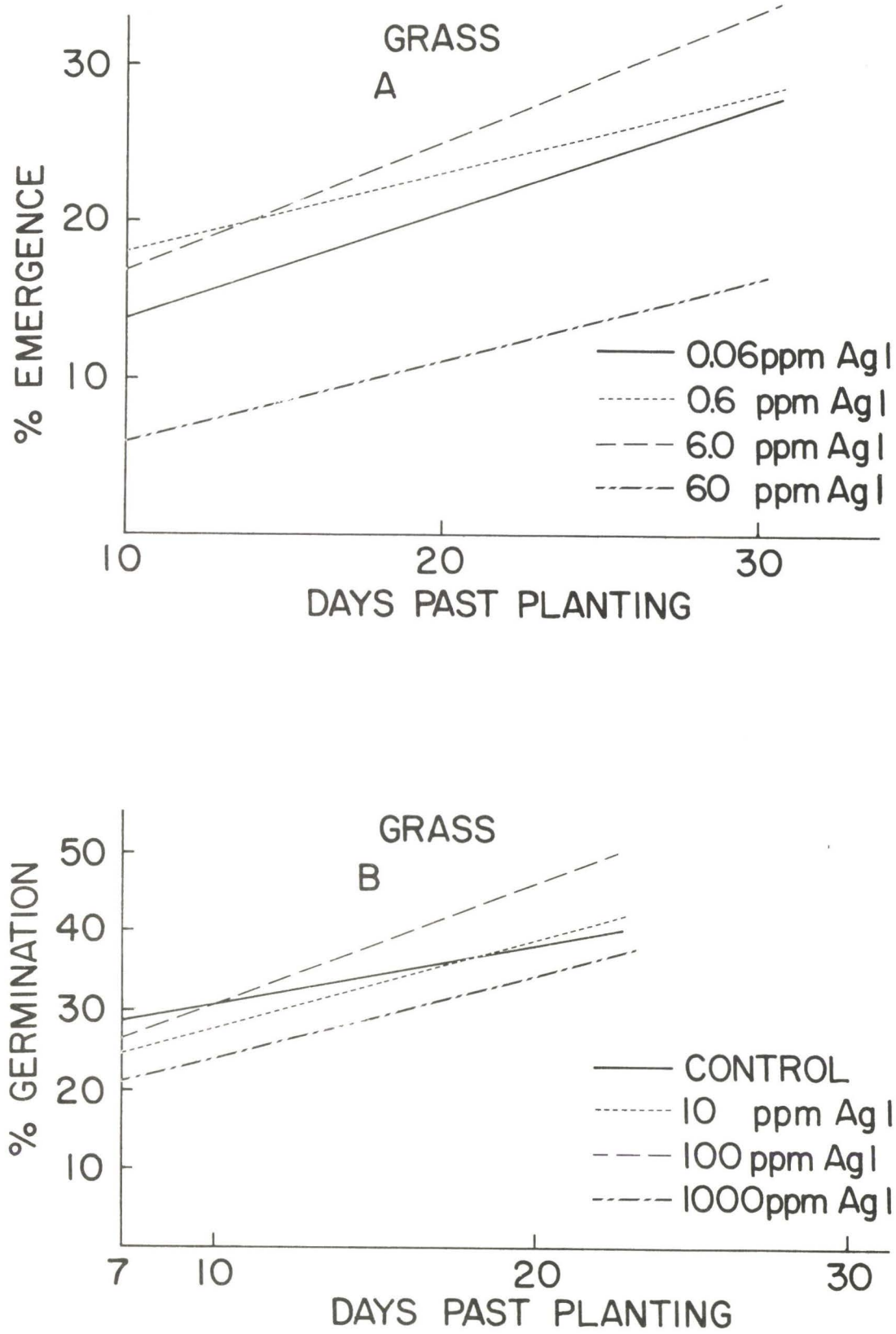

Fig. 66. The percentage emergence (A) and germination (B) of tufted hairgrass at days past planting for 4 Agl treatments.

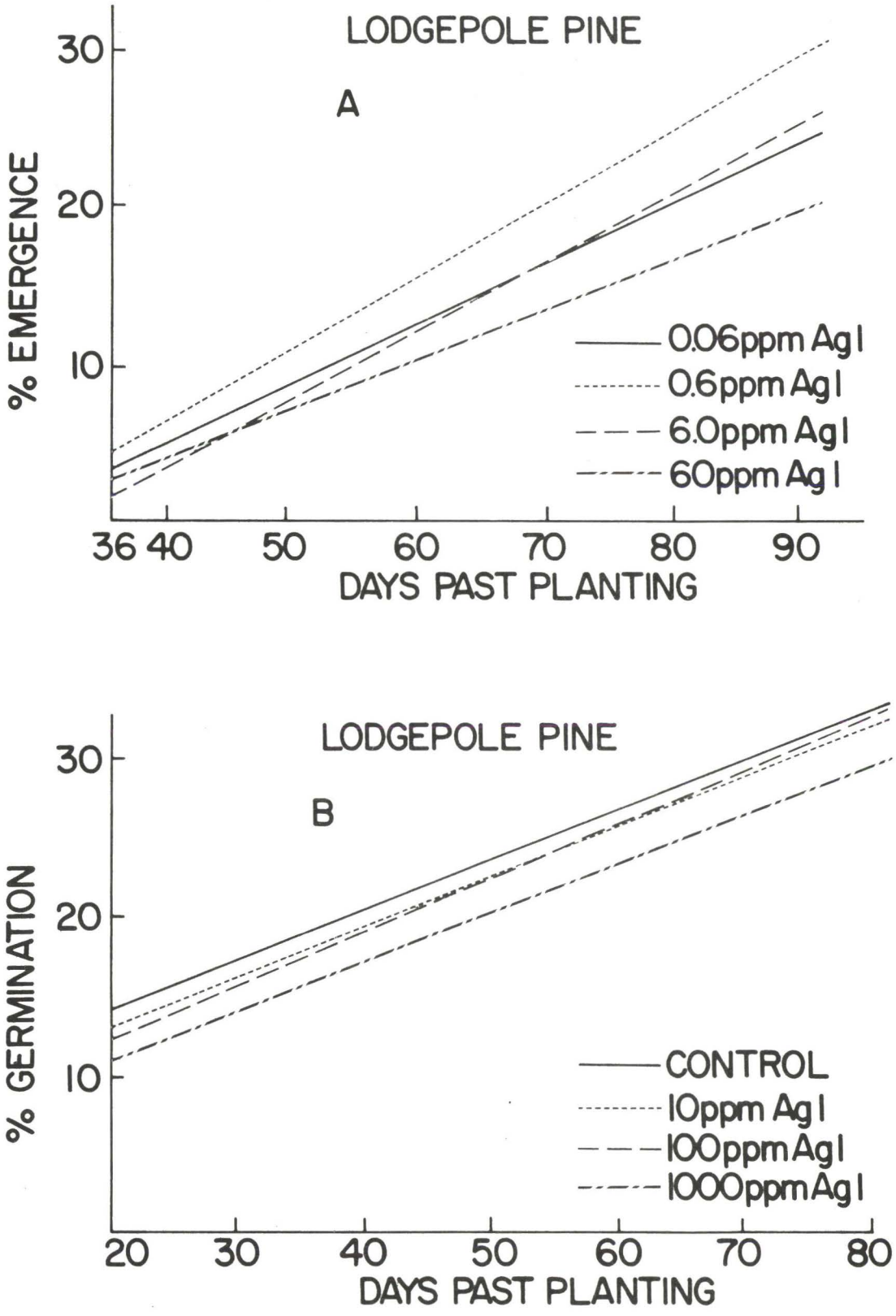

Fig. 67. The percentage emergence (A) and germination (B) of lodgepole pine at days past planting for 4 AgI treatments.

were higher than could possibly be found in natural or even cloud seeded areas. The 1,000 ppm silver treatment lowered germination percentages compared to the other three treatments for both species, although not at a significant level. The possibility of concentrations reaching high enough levels to affect germination is remote, but the effects on emergence could occur when concentrations of silver approached the 60 ppm level. This concentration is not likely to occur from cloud seeding with silver iodide over wide areas, but it could be important close to the generators.

Fig. 68 shows the 15 pots for each treatment for lodgepole pine. Very little visual difference can be seen between the four treatments, but close observation reveals a smaller growth size in the 60 ppm group. Fig. 69 shows the total yield, yield of roots, shoots, and root-shoot ratio of lodgepole pine under the four treatments. Treatment D, 60 ppm Ag, produced significantly less total weight in roots and shoots than the three other treatments.

The shoot-root ratio for lodgepole pine increased with added Ag, although none of the treatments were statistically different at the .05 level. This suggests that as the silver concentration increased less root growth occurred in the small lodgepole pine seedlings.

It is interesting to note that treatment B (0.6 ppm) increased production, although it was not significantly greater than the other three treatments at the .05 level of significance. It is possible that the NH_4I which was added with the AgI could have had a fertilizing effect on the growth of the plants, but this seems rather remote when one considers that treatment C (6.0 ppm AgI) received more NH_4I than did treatment B (0.6 ppm AgI) and the growth of the plants was about the same in treatment C as in treatment A (.06 ppm AgI) which received no NH_4I.

Fig. 70 shows the total yield, yield of roots, shoots, and shoot-root ratio of tufted hairgrass. As in lodgepole pine, 60 ppm silver affected total production as well as the production of shoots and roots. Note for tufted hairgrass that the different levels of

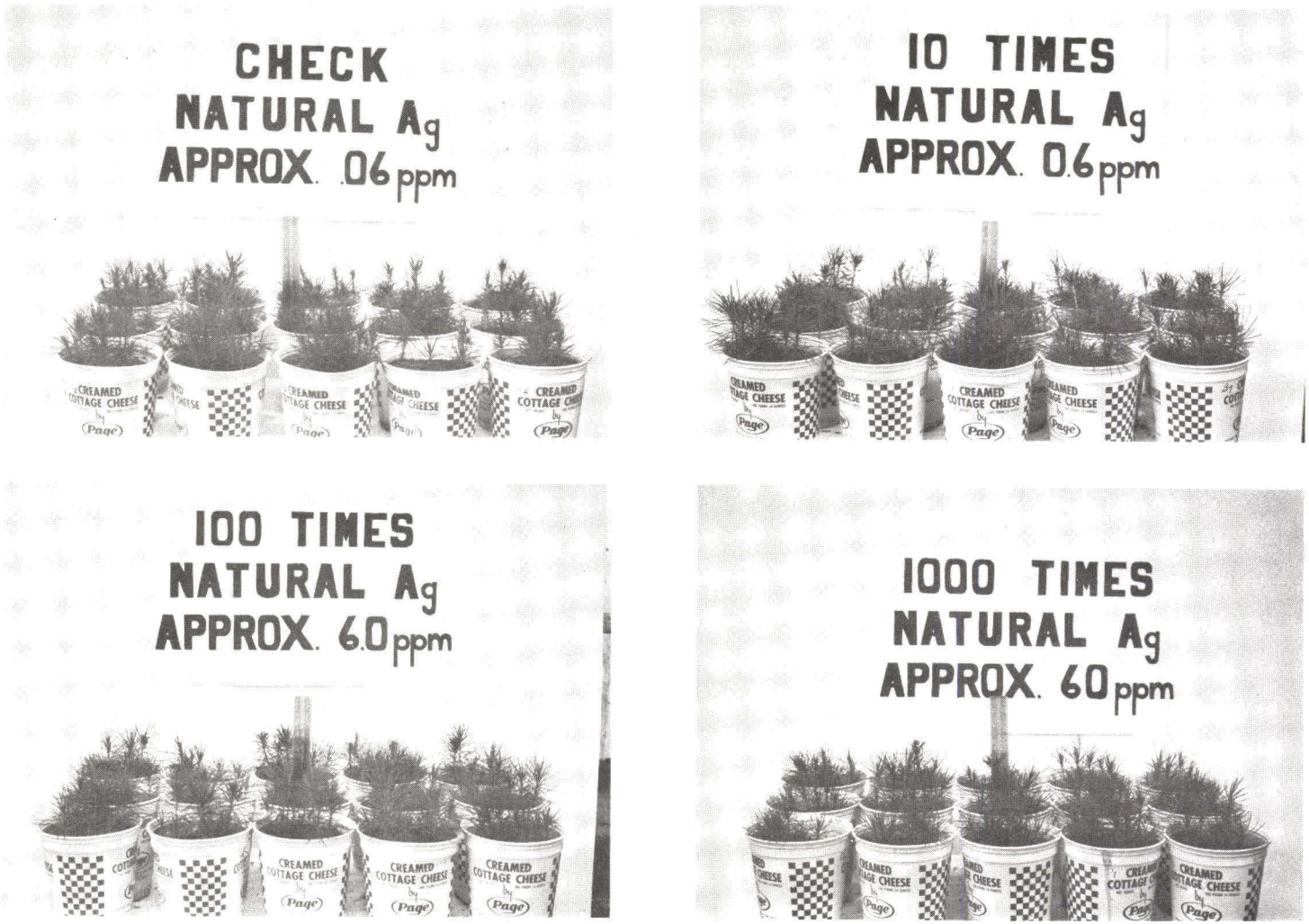

Fig. 68. Photographs of the 15 replications for each AgI treatment in the lodgepole pine greenhouse experiment.

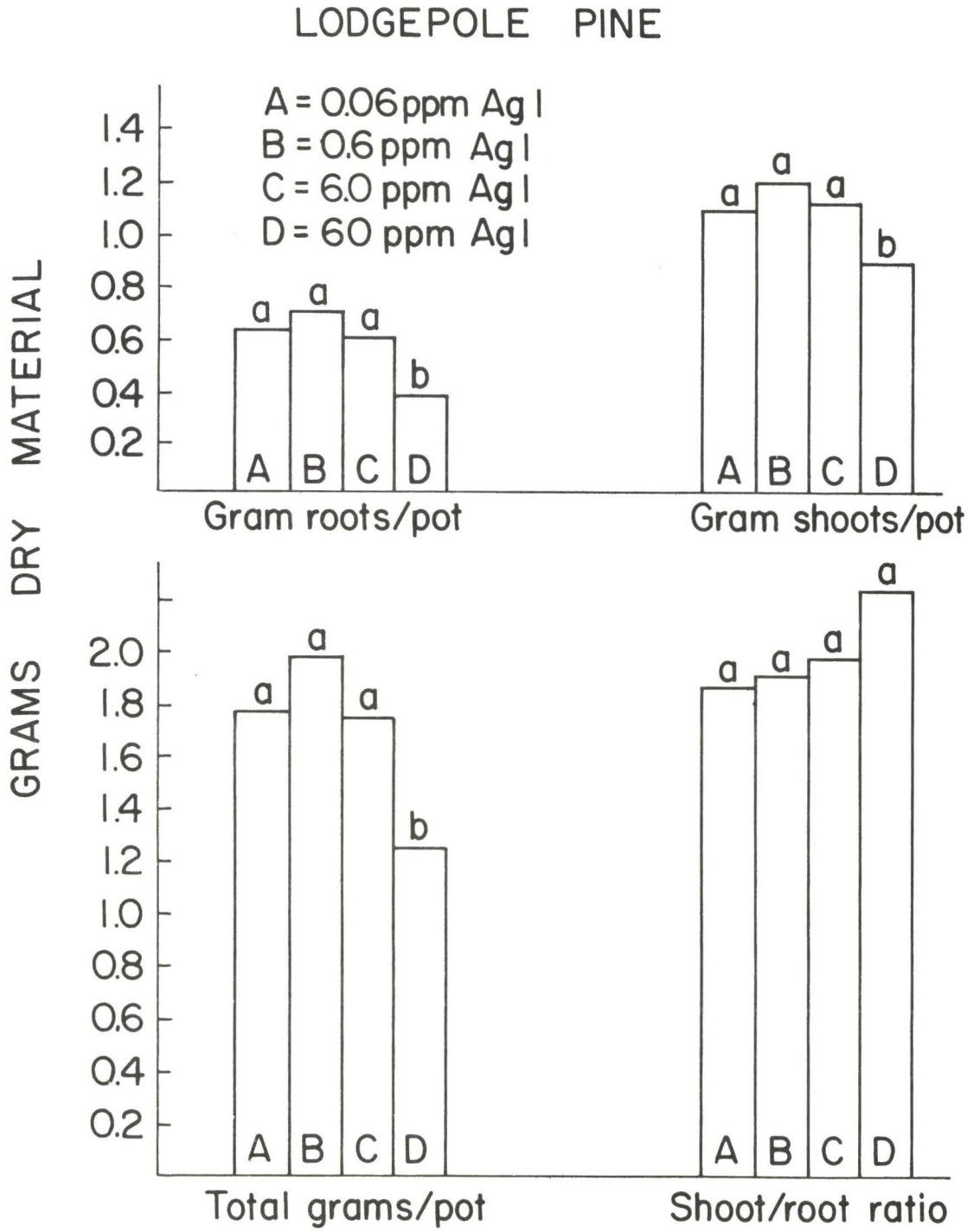

Fig. 69. Total yield, root yield, shoot yield, and root-shoot ratio of lodgepole pine seedlings as affected by different levels of AgI applied to the soil. Bars labeled with the same letter are not significantly different (0.05). Bars are the averages of 15 observations.

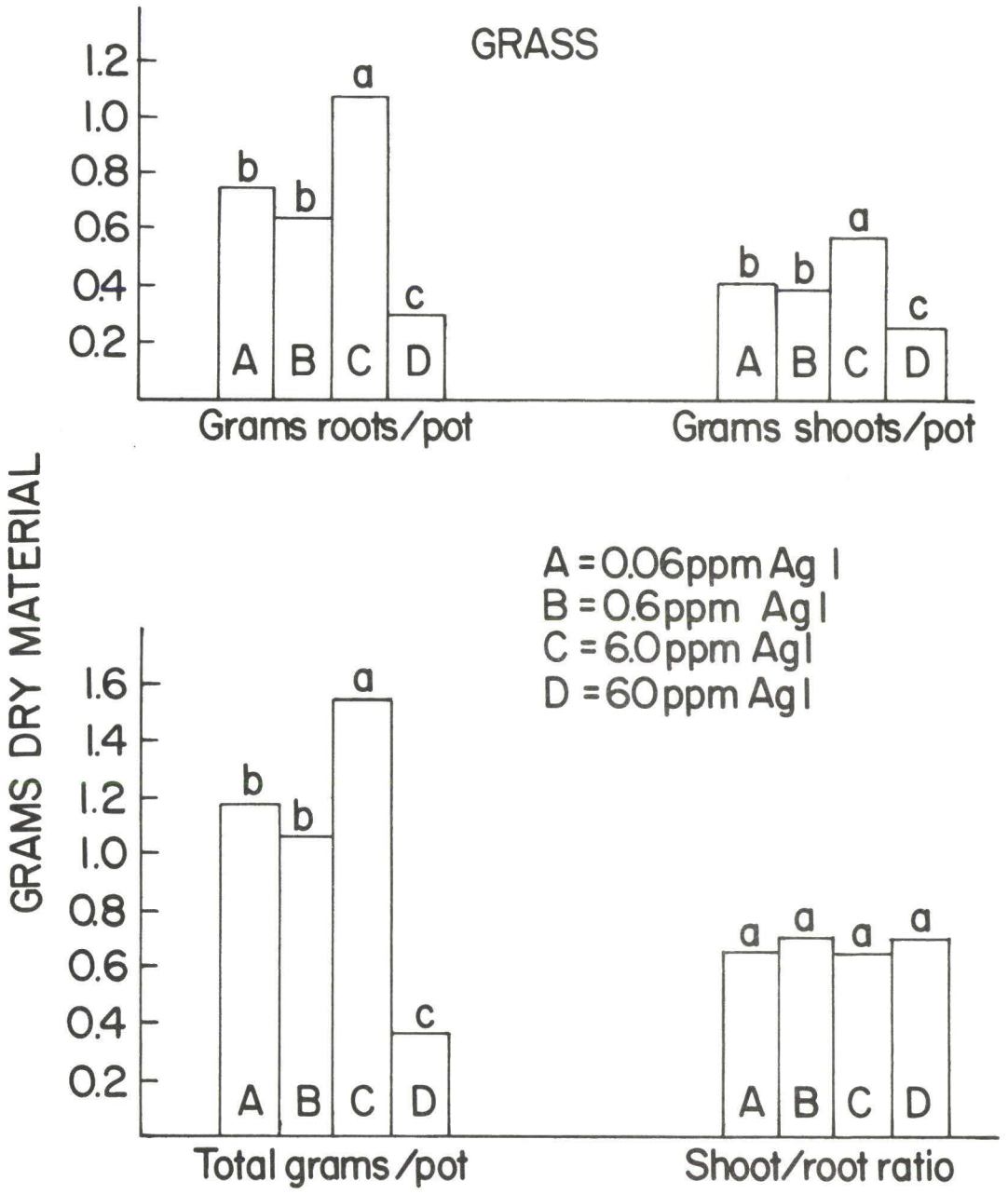

Fig. 70. Total yield, root yield, shoot yield, and root-shoot ratio of tufted hairgrass as affected by different levels of AgI applied to the soil. Bars labeled with the same letter are not significantly different at the 0.05 level. Bars are the averages of 15 observations.

silver had very little effect on the shoot-root ratio. The various levels of AgI affected the shoots and roots of tufted hairgrass in a similar manner. This observation is in contrast to lodgepole pine in which roots were more affected by higher levels of AgI added. Treatment C (6.0 ppm) showed significantly greater production of roots, shoots, and total weight than the other three treatments. This contrasts with lodgepole pine in which there was an increase in production at the 0.6 ppm treatment of AgI, although not at a significant level (.05).

Comparison of data in the germination and emergence study with the growth data reveals that a relationship exists between percentage emergence and total production. In tufted hairgrass, for instance, 60 ppm AgI resulted in significantly less percentage emergence and 6.0 ppm AgI caused an increase in percentage emergence although not a significant increase at the .05 level. A correlation with production data is evident; 60 ppm AgI resulted in a significant decrease in total production, while 0.6 ppm caused a significant increase in total production. We conclude that production of tufted hairgrass under the higher AgI treatments was reduced primarily because the plants had lower percentage emergence, although there was a difference in the size of the plants due to treatment.

In lodgepole pine, the 0.6 ppm treatment was greater for both percentage emergence and total production, although not significantly at the .05 level in either case. The 60 ppm AgI treatment, however, significantly reduced both percentage emergence and total production. Fig. 68 shows that plants subjected to the 60 ppm treatment were somewhat smaller in size. We postulate that the effect of AgI on total production is due to the combined effect on plant size and percentage emergence.

Uptake of Ag. Table 69 shows that lodgepole pine accumulated more Ag in its foliage than did tufted hairgrass, when grown in soil containing only natural Ag (approximately 0.06 ppm). These data correpond to those obtained from field samples of lodgepole pine

and grass collected under natural soil conditions (previously reported on p. 10).

Table 69. Uptake of silver of plants in greenhouse study, reported in ppm dry matter. Each mean is the average of three observations. Means not labeled with the same letter in each column are significantly different at .05 level.

Treatment	Lodgepole Pine	Tufted Hairgrass
.06 ppm	.87 a	.27 a
.60 ppm	1.33 a	3.85 a
6.0 ppm	2.15 b	4.67 a
60.0 ppm	3.09 c	51.77 b

In natural environments, silver uptake by terrestrial plants has been reported to range from 0.07 ppm dry matter in gymnosperms to 9.0 ppm in bryophytes and even up to several hundred ppm in mushrooms (Cooper and Jolly 1969). Lounamaa (1955), working in Finland found that plants frequently have a higher concentration of silver than their associated soil and substrate. He reported concentrations up to 30 ppm dry weight in forest trees. Teller and Cameron (1972) reported values of 0.01 ppm Ag on a dry weight basis for spruce, aspen, and grass foliage in the San Juan Mountains of Colorado.

Tufted hairgrass accumulated more silver than did lodgepole pine in all treatments except the control. For the highest treatment (60.0 ppm Ag), tufted hairgrass accumulated 51.77 ppm Ag compared to 3.09 ppm for lodgepole pine. This corresponds with regression data presented on page 14 which indicate that grass would accumulate more Ag than lodgepole pine under increased soil Ag concentrations.

For lodgepole pine the 6.0 ppm treatment accumulated significantly more silver than did the two lighter treatments 0.06 and 0.6 ppm (Table 69). The 60 ppm treatment accumulated significantly more

silver than the other three treatments. The data indicate that Ag accumulation will increase with an increase in the availability of Ag in the soil.

Conclusion

In conclusion, it seems unlikely that the addition of AgI by cloud seeding would have an undesirable effect on soils, plants, or water in the near future, except perhaps in the immediate vicinity of AgI generators. Our data suggest that the amount of AgI added to the soil by cloud seeding will not have adverse effects on lodgepole pine and tufted hairgrass seedlings (and probably other associated plants) until the concentrations are 100 to 1,000 times greater than those naturally found in the soils of the Medicine Bow Mountains. As described previously, we estimate that it would take approximately 450 years of cloud seeding to double the natural soil concentration.

Silver deposited on land surfaces is immobilized in the top few centimeters of soil, so there should be little movement of Ag to the ground water directly. Runoff and soil erosion, which are considerable in the Medicine Bow Mountains as seen in the murky water of spring, could contribute to the Ag content of streams and lakes. (We have not studied Ag concentrations in the aquatic ecosystems of the Medicine Bow Mountains.) Once the concentration of Ag in the soil is doubled or tripled, the rate of surface accumulation of Ag could increase due to increased uptake by plants and subsequent deposition on the surface in plant residue. In this way more Ag could become available for surface runoff, but we do not know what the significance of this factor would be to either aquatic organisms or to terrestrial organisms in depressions where the Ag may accumulate more rapidly than otherwise expected.

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SILVER IODIDE: ACUTE TOXICITY, TISSUE DISTRIBUTION, AND SUBCELLULAR DISTRIBUTION IN RAINBOW TROUT

A. D. Anderson and M. R. Huff

Silver concentrations in seeded storms have been reported to be about 0.1 µg per liter, which is about ten times the concentration of unseeded storms (Cooper and Jolly 1970). Silver is the most toxic (Jones 1964, Jones 1971) and the least studied (Coleman and Cearley 1974) of the heavy metals in aquatic ecosystems.

Although silver has been considered to be non-toxic to aquatic life at low levels, silver nitrate has been shown to be acutely toxic at concentrations above 3 to 5 µg silver per liter (Anderson 1948, Jones 1964). The threshold of toxicity of silver nitrate to rainbow trout has been reported to be between 0.09 and 0.17 µg per liter (Goettl, Sinley and Davies 1974). Silver iodide is soluble at 0.3 µg per liter (Goettl, et al. 1974).

Possible toxic effects of silver on the development and growth of fish have been reported. Wilbur (1969) found silver nitrate to be toxic to fish eggs at 10 µg per liter. The possible effects of silver iodide on rainbow trout eggs, however, are apparently hidden by the addition of sodium iodide (Goettl, Sinley and Davies 1974) needed to solubilize the silver iodide. Long-term studies by this same research group have shown that silver nitrate and silver iodide without a common anion cause premature hatching of eggs and developmental retardation. It has been reported that when the silver concentration increases, the rate of growth decreases (Coleman and Cearley 1974).

Silver has been reported to accumulate in the kidney and liver of gold fish (Hibiyta and Oguri 1963) and in the internal organs of the bass and blue gill (Coleman and Cearley 1974) at concentrations (0.3 to 70 µg/l) greater than that of the exposure water. An increased

accumulation was reported with an increased exposure time, and it was observed that silver may replace divalent cations normally present as enzyme cofactors.

Methods

Rainbow trout from the Wyoming State Fish Hatchery at Como Bluffs were used for our studies. These fish are common in the Medicine Bow Mountains. In a typical experiment, 300 to 350 trout (10 to 15 cm) were divided among six fish tanks. It was determined that stainless steel fish tanks are best suited for the toxicity uptake studies, since silver was less readily adsorbed onto the tank. Six 18-gauge stainless steel tanks were used (122 x 61 x 30 cm). The aquaria were operated under a diluter for maintaining a series of constant concentrations of silver salts in 8,640 l of flowing water per day. The diluter, called a proportional diluter, is based on simultaneous dilution of one concentration. Mount and Brungs (1967) have described the proportional diluter we used in our system. Three heat exchangers were used to cool the water to $8^{o}C \pm 1^{o}C$.

The purity of the water in the aquaria was monitored along with the temperature, dissolved oxygen concentration, and pH. Organic foreign material and chlorine were removed by means of an activated carbon filtration system.

The concentration of silver in the water was adjusted so that the toxic effects of different concentrations could be studied. A teflon-lined container was used for the toxicant-measuring apparatus. It was determined that teflon prevented silver from plating out on the container.

One problem with silver iodide is its insolubility in water at low concentrations. Potassium iodide, ammonium iodide and sodium iodide have the ability to improve the solubility of the silver iodide and were used for this purpose in most of our experiments. Silver iodide was added to the feed by dissolving the AgI in 2 M potassium iodide. The iodide (being the common anion) forced the silver iodide

into a suspension or complexed state. This suspension was then mixed with the feed and given to the fish. The various feeds contained a constant amount of potassium iodide; the concentrations of silver iodide were as follows: 10.0, 5.0, 1.0, 0.5 gm per kg of feed with two controls containing only potassium iodide. The amount of feed given to the fish was 5 g/kg fish/feeding; the fish were fed twice a day.

For the ^{110M}Ag radioisotope uptake studies, two ten (10) gallon glass fish tanks were placed in two of the stainless steel tanks described above. The temperature in the smaller static tanks was maintained at $8^{o}C \pm 1^{o}C$ by circulating cool water thru the larger tanks as described previously. In order to minimize the accumulation of toxic waste products, only one fish was placed in each 10 gallon tank.

Radioactive silver (^{110M}Ag) nitrate and silver (^{110M}Ag) iodide were employed to study the regional and subcellular uptake of silver nitrate and silver iodide, respectively. The fish were exposed to 150 μC of ^{110M}Ag in 40 l of water for 96 hours. The fish were then anesthesized by ice and dissected. The various tissues were weighed and counted in a Packard 3001 gamma counter.

A subcellular distribution of ^{110M}Ag in muscle was conducted after the trout were subjected to silver (^{110M}Ag) iodide for 96 hours. Muscle tissue was weighed and a sufficient amount of 0.25 M sucrose was added to make a 20% solution. This solution was homogenized and centrifuged at 300 x g for 15 minutes. The resulting supernatant fluid was centrifuged at 10,000 x g for 20 minutes. After the 10,000 x g spin the supernatant fluid was decanted and centrifuged at 100,000 x g for 60 min. The homogenate, 300 x g supernatant fluid, 10,000 x g precipitate (mitochondria), 100,000 x g supernatant fluid, and precipitate (microsomes) were counted. Protein assays were conducted on each of the above samples and specific activities calculated.

Results and Discussion

Toxicity of Silver Iodide in Feed

Table 70 shows that silver iodide was not toxic to fish in concentrations of up to 10 g silver iodide per kg of feed. The only problem with this experiment was that the fish did not eat the feed as well if potassium iodide had been added. However, the potassium iodide concentration was constant in all tanks, including the control tanks.

TABLE 70. Toxicity of Silver in Fish Feed.

Experiment	Time	Results						
Feed coated with AgI-KI, 8-15 cm fish, 8°C ± 1	41 days	conc.: KI	0.8	0.8	0.8	0.8	0.8	M
		AgI	10	5	1	0.5	0	gm/kg feed
		ratio $\frac{\text{dead}}{\text{total}}$	$\frac{0}{60}$	$\frac{1}{60}$	$\frac{1}{60}$	$\frac{2}{60}$	$\frac{5}{60}$	fish / fish
$AgNO_3$ added to the water after 41 days of feeding 10 gm silver per kg feed	15 days	conc: $AgNO_3$	100	50	25	12.5	6.25	0 µg/l
		ratio $\frac{\text{dead}}{\text{total}}$	$\frac{48}{48}$	$\frac{50}{50}$	$\frac{55}{55}$	$\frac{59}{59}$	$\frac{0}{60}$	$\frac{1}{60}$ fish

Silver iodide was found to be non-toxic when mixed in the feed as a common salt with potassium iodide.

Fish exposed to silver iodide in their feed were later exposed to silver nitrate (Table 70). The 24 hour LC_{50} for silver nitrate without previous exposure to silver iodide was determined to be 10.1 µg/l. The 24 hour LC_{50} for silver nitrate, in which the fish were previously exposed to silver iodide in their feed, was above 100 µg/l and the 120 hour LC_{50} was 11.5 µg/l. These results suggest that the silver iodide in the fish food protected against the acute toxicity of silver nitrate.

Toxicity of Silver Iodide in Water

Silver iodide with potassium iodide in water probably has no short term effect in concentrations of up to 1 mg/l (Table 71). This is possibly over a thousand times the concentration the fish would be exposed to after many years of cloud-seeding, since the concentration in the environment after cloud-seeding probably will be in the range of 100 ng/l. We conducted an experiment to determine if concentrations of up to 1 mg/l silver iodide with potassium iodide had any long term effects on infant fish and eggs. After initial exposure, the fish and hatched eggs were kept under observation in clear water for 75 days. During this time there were no observable effects on the growth of the fry.

The 24-hour LC_{50} for silver nitrate without previous exposure to silver iodide was determined to be 10.1 µg/l. The 24-hour LC_{50} for silver nitrate in which the fish were previously exposed to up to 1 mg silver iodide per 1 was above 100 µg/l and the 120-hour LC_{50} was 13.7 µg/l. The 24-hour LC_{50} for silver nitrate in which the fish were previously exposed to up to 10 mg silver iodide per 1 was 21.2 µg/l. These results suggest that silver iodide and/or potassium iodide protect(s) the fish against the toxicity of silver nitrate. Silver nitrate was less toxic after silver iodide exposure.

In two experiments, 1 mg/l silver iodide was not toxic in fourteen days, however, in the third experiment silver iodide was toxic at 1 mg/l, i.e., the fourteen day LC_{50} was 1.7 mg/l. The discrepancy was probably due to the final ratio of potassium iodide to silver iodide in the tanks.

In control experiments we found that sodium iodide and potassium iodide were not toxic at the concentrations we used, though Goettl, et al. (1974) found they were toxic at higher concentrations. This is probably due to KI shifting the equilibrium of the $AgI \rightleftharpoons Ag^{+} + I^{-}$ to the left, the KI providing the excess I^{-}. The presence of silver in the tanks at the expected concentration was verified using atomic absorption spectroscopy.

TABLE 71. Toxicity of silver in water.

Experiment	Time	Results						
AgI - NaI, 8-13 cm fish, 8°C ± 1	16 days	conc.:	1000	500	250	125	67.5	0 µg/l
		ratio dead/total	0/36	0/36	0/36	0/36	0/36	0/36 fish
		Comments: Wyo. State Lab analysis of Ag concentration in tanks yielded 1100, 490, 280, 140, 90 and 0 ppb						
$AgNO_3$ toxicity on fish from above	8 days	conc.:	100	50	25	12.5	6.25	0 µg/l
		ratio dead/total	31/31	35/35	27/32	7/29	0/36	0/36 fish
AgI - KI, 8-13 cm fish and eggs, 8°C ± 1	14 days	conc.:	1000	500	250	125	67.5	0 µg/l
		Comments: no fish died and all eggs hatched within 5 days; none of the fry died.						

Table 72 presents the chronologic results of another experiment to determine the sensitivity of trout to various concentrations of Ag (added as AgI - KI) in water. In this case the 7-day LC_{50} was 7.6 mg/l, the 14-day LC_{50} was 1.7 mg/l, and the 21-day LC_{50} was 1.3 mg/l.

TABLE 72. Acute toxicity of AgI - KI. Values are the percent of 100 fish that died after 3 time intervals at different concentration of AgI.

	AgI concentration in mg/l					
	10	5	2.5	1.25	0.625	0.0
Week 1	54	22	20	9	3	0
Week 2	100	95	70	44	9	2
Week 3	100	99	84	53	12	3

Dr. Don Klein kindly provided effluent from a cloud seeding apparatus. Although there was only enough effluent to run a six-hour experiment, no toxicity was observed. In a typical experiment we used 43.5 g silver iodide and 332 g potassium iodide every six hours. Such large amounts of silver iodide are difficult to obtain from cloud-seeding effluent.

Tissue and subcellular distribution of ^{110M}Ag

The ^{110M}Ag present in solution (0.13 µg Ag per liter) as silver nitrate was found to accumulate mainly in the liver, Table 73, with minor accumulations in the gall bladder, kidney, gills and intestine. Other tissues measured contained about 1/1000 that of liver or less. Others have reported similar accumulation data with other aquatic life. It is interesting to note, however, that the ^{110M}Ag present in solution as silver iodide (0.13 µg Ag per liter) accumulated mainly in the intestine. The only explanation for these results would be that iodide and/or nitrate anions affect the accumulation of silver in fish.

Since silver present as silver iodide was preferentially taken up into microsomes (Table 74) and since the microsomes are responsible for protein synthesis, it is not unexpected that silver iodide without another iodide salt causes retardation of growth and premature hatching of fish eggs (Goettl, Sinley and Davies 1974b). It is well known that the silver ion will titrate sulfhydral groups of proteins and cause enzyme inhibition and denaturation. It is interesting that the uptake of silver into microsomes and mitochondria may cause abnormalities in protein synthesis and cellular respiratory distress.

TABLE 73. Tissue distribution of ^{110M}Ag in rainbow trout.

Tissue	Silver Iodide count/g/min*	Silver Nitrate count/g/min**
Heart	378.00	75.03
Liver	81.50	61,600.49
Gallbladder	366.45	669.64
Stomach	114.93	37.53
Spleen	81.60	68.50
Kidney	144.38	1,088.20
Gills	106.25	1,355.95
Blood	94.50	14.64
Brain	260.05	64.97
Tissue with Skin	98.44	3.26
Intestine	1,229.55	250.87
Fat	206.70	22.24
Deep Tissue	67.30	-----
Bone	80.90	-----
Food (stomach)	1,690.00	-----
Food (intestine)	434.30	-----

* Averages of two experiments, expressed as counts per g wet weight of tissue.

** Averages of 3 experiments, expressed as counts per g wet weight of tissue.

TABLE 74. Subcellular distribution of ^{110M}Ag in skeletal muscle of rainbow trout.

Subcellular fraction	^{110M}Ag Counts per min per mg protein*
Homogenate	1.02
300 x g precipitate	0.016
Mitochondria	1.12
Microsomes	1.45
100,000 x g supernatant fluid	0.82

* The values are the average of two experiments.

CONCLUSION

These results demonstrate that silver iodide, with another iodide salt, is not toxic to rainbow trout in a concentration which is likely to occur with cloud seeding activities in the near future. It is probably by providing a common ion, I^-, that potassium iodide protects against silver iodide toxicity with the short-term exposures used in this study. Even though preliminary toxicity studies performed using only silver iodide indicate that it is toxic at very low concentrations (Goettl, et al. 1974b), studies on the environmental ratio of silver iodide to iodide ion (and other monovalent anions) are needed to evaluate potential ecologic significance. Since silver iodide is used as a nucleating agent with a common ion, it is probable that a non-toxic form of silver iodide is actually produced by AgI generators. The effects of other environmental anions on silver toxicity should be studied, since these anions could decrease silver toxicity.

Another consideration for continued study may be the possible interaction of silver with other metals. Since many enzymatic reactions take place with the aid of trace amounts of metals (e.g., copper and zinc), an accumulation of silver may alter the metabolism of the fish (Coleman and Cearley 1974).

When silver iodide and potassium iodide are mixed with fish food, it is not toxic to rainbow trout even at very high concentrations. It has not been shown that silver iodide changes form in the food chain, so silver iodide is probably not toxic to trout in their feed.

We have shown that silver from silver iodide is taken up preferentially into microsomes and mitochondria of rainbow trout. Silver iodide is accumulated in the intestine while silver nitrate is accumulated in the liver, gill and kidney. It is interesting that silver was taken up by the trout even when silver iodide is at concentrations of only 0.14 µg silver per liter.

The silver from silver iodide probably is taken up through the intestine of fish because of the high concentration of silver in the stomach contents and low concentration of silver in the intestinal

contents. The silver iodide is probably adsorbed from the fish food and concentrated in the intestine.

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GENERAL DISCUSSION

Dennis H. Knight

Since about 1966 ecologists and others have written about the potential problems that reasonably could occur as a result of intentional weather modification (Livingstone et al. 1966, Nat'l. Acad. Sciences 1966, Waggoner 1966, Malone 1967, Sargent 1967, Whittaker 1967, American Meteor. Society 1968, Douglas 1968, Pierce 1968, Cooper and Jolly 1969, 1970, Weisbecker 1972). For the most part these studies have been speculative in nature, but have been very valuable for arranging research priorities (particularly Cooper and Jolly 1969 and Weisbecker 1972). The Medicine Bow Ecology Project was not intended to repeat or review the speculative efforts of these authors, but rather to conduct research that would provide a basis for deciding the probability that some of the predicted problems would in fact be experienced in a specific area -- the Medicine Bow Mountains. Other studies similar to ours include those of Collins, Super, and Weaver in Montana (see Weaver 1974 and Weaver and Super 1972 for several references), the San Juan Ecology Project in Colorado (final report to the Bureau of Reclamation in preparation), and a study on summer rainfall augmentation in eastern Wyoming (Becker et al. 1973). Thus, ecological research on weather modification is progressing through the logical phases of 1) conducting potential problem analyses, and 2) conducting research to determine better the probability that the potential problems of greatest concern will occur.

The studies of Whittaker (1967), Cooper and Jolly (1969), and Weisbecker (1972) reveal that there are many changes that could occur as a result of cloud seeding. It has not been possible for us, nor any other research team thus far, to study all of the potential effects in the time available. In fact, the total analysis of any ecosystem is not yet possible. Decision makers are thus in the position of having to rely on the best available information and speculation. The situation would not justify making a national, long-term commitment to intentional weather modification, but it should not prevent

the pursuance of exploratory pilot projects if 1) the probability of problems seems low, 2) the benefits appear to outweigh the costs, and 3) the project can be cancelled if unexpected problems occur. The indirect effects of management on ecosystems are the most difficult to predict and may be the major source of problems.

The accurate evaluation of the potential ecological impact in an area of snowpack augmentation is possible only if accurate projections are available on 1) how much snow will be added, 2) how long snow cover will be prolonged, 3) how much AgI will be added per year to the ecosystems, and 4) whether or not other environmental modifications will occur, such as increased cloudiness. We have come to our conclusions on the basis of what appear to be generally held assumptions, namely, that snowpack will be increased by about 15 percent only during less than maximum snowfall years, that an additional 15 percent of snow will prolong snow cover for only about 3 days, that snowfall will not be affected below about 2700 m, that it will take several hundred years to even double the natural Ag concentrations in the soil by seeding, and that little or no increased cloudiness will occur as a result of seeding. If these assumptions are greatly in error, then our evaluation of impact will be in error.

Changes in natural ecosystems can be expected as a result of cloud seeding. As Whittaker (1967) writes,

> "Changes in rainfall or temperature of sufficient magnitude to have substantial usefulness to man seem likely also to be of sufficient magnitude to produce disturbance in natural communities."

Changes occur in ecosystems for a variety of reasons, however, e.g. by controlling fire, cutting trees, grazing by domestic livestock, heavy recreational use, road construction, pest control, fertilization, etc. Some changes may not be acceptable, e.g. the creation of dirty stream water with toxic levels of heavy metals; other changes may be undesirable but acceptable if the benefits are sufficiently high, e.g. a shift in the species composition of a meadow; and still other changes may be so slight that they are hardly noticeable or they are desirable for some

people. The danger in modifying environmental characteristics for the benefit of man, by whatever method, is that all other native plants and animals in the area are adapted to the original environment, in which they evolved, and some may not be able to adapt to the new environment created by man. These plants and animals are part of the life support system on which man depends. Furthermore, the changes that initially seem to the benefit of man may in the long term be to his detriment, perhaps because living in the new environment calls for still greater fossil fuel demands, or, in the case of additional water from cloud seeding for irrigation, increased salinization problems downstream from the fields. Weisbecker (1972) suggests that cloud seeding will increase the salinity of the Colorado River partly by the additional water moving through the soil and partly by the use for irrigation of the additional water. The latter examples illustrate how the undesirable effects of cloud seeding may be felt some distance from where the additional snow actually falls. We have studied only some of the potential local effects; the indirect "downstream" effects may be more important. Also, we have studied only the effect of cloud seeding. With changes occurring as a result of so many other human activities, questions now arise about the combined effect of all influences. For example, what will be the effect on stream water quality of cloud seeding over a watershed that has been 10 percent clearcut, has 2 picnic areas, 12 miles of roads, and was fertilized 3 years ago to promote tree growth? This kind of question should be addressed also, but in most areas it is first necessary to obtain data on the ecological effects of individual management activities.

The information we have gathered from the Medicine Bow Mountains must now be integrated, to whatever extent possible. First, all changes that occur in the Medicine Bow Mountains as a result of cloud seeding are likely to be slow. The ecosystems will not be subjected to any immediate perturbation which they do not already experience periodically, with the possible exception of a very small addition of AgI each year which we do not believe will in the near future modify any existing ecosystem components or processes, except perhaps adjacent

to generator sites. Over the years, however, Ag and I will accumulate and may be concentrated by natural ecosystem processes. Accumulation will occur first in the litter and surface soil, where Ag could affect the decomposition process sufficiently to modify patterns of nutrient cycling. We know that Ag accumulates there and we know bacteria and fungi are sensitive to low concentrations of Ag, but we do not know the extent to which nutrient cycling would be affected, if at all. It is doubtful that Ag accumulation will have any effect on trout or plant growth in the next several hundred years or more, unless natural processes concentrate the Ag to toxic levels. This possibility should be studied, since we have observed that the Ag may move in surface runoff and may be accumulated in some plants. With regard to the other potential effects of AgI, we know no more than has been summarized by others (Cooper and Jolly 1969, 1970; Weisbecker 1972). The actual number of planned generator sites should be known in future studies on the potential rate of Ag accumulation.

Vegetation would be affected very slowly, and with no undesirable shifts in species composition of which we are aware. The changes would occur as shifts in abundance, rather than the complete disappearance of any species. We do not think the changes in vegetation would be to the detriment of wildlife. Our research did not include the tree component, however. Results on tree sensitivity from the San Juan Ecology Project may be applicable to the Medicine Bow Mountains.

Both the terrestrial and aquatic vegetation of the region could be affected by the nutrient losses and gains resulting from increased water flow through the montane ecosystems. The terrestrial habitats could lose nutrients by leaching more rapidly than nutrients are gained by weathering and other sources, and downstream lakes could gain nutrients more rapidly than they're lost, thereby leading to eutrophication. However, because the flushing rate of the montane lakes is so rapid, the eutrophication would occur farther downstream. Research is recommended to determine the effect of an increase in mean annual water flow through the ecosystem on terrestrial and aquatic nutrient availability. Since the nutrients added to downstream reservoirs and

lakes could come from so many sources, the potential loss of nutrients from the mountain soils should be studied first. If more water moves through these soils, more nutrients will be lost. Since the maximum amount of water flow per year will presumably not be changed by cloud seeding, the question relates more to the effect of an increased mean annual water flow.

The timing of cloud seeding is important for the general well-being of deer, elk, and winter range vegetation. Because winter range is already a limiting factor in the area, deer and elk should not be forced to spend any more time on the winter range than is necessary due to natural snowfall patterns. Cloud seeding should not be done in the fall or spring, thereby promoting fall migration or postponing spring migration, and cloud seeding would not be recommended by wildlife managers if snowfall increases on the winter range.

Because the montane lakes and streams are already subjected to drastic changes in water level during the year, cloud seeding is not likely to cause great changes. A mean annual increase in stream water flow could reduce the mean annual water temperature, thereby slowing fish and plankton growth still further, but the magnitude of this effect is not known and other factors may be more limiting than water temperature.

One of the more subtle effects of cloud seeding may be to reduce the year-to-year variability in growing season length. Our data on Vaccinium scoparium, and theoretical considerations, suggest that an occasional long growing season may be important for the survival of some plants, and probably some animals, in areas where growing season length is a limiting factor, e.g. the Medicine Bow Mountains. The problem may be non-existent if cloud seeding is not used during normally high snowfall years and if it is impossible to produce additional snowfall by seeding during low snowfall years, as some suggest. The extreme low snowfall year may not be as necessary to the plants as years that are, say, 50 percent below average. Seeding could reduce the frequency of these below-normal years, which could be another cause of slow ecosystem changes.

The opinion has been expressed frequently that additional snow from cloud seeding will not prolong snow cover for any given year, which would tend to negate any effect of cloud seeding on growing season length. Haeffner and Leaf (1973) write, "....winter snow accumulation higher than normal apparently does not delay the disappearance of the last snow." If this is true, and snowfall is increased only above 2700 m, then cloud seeding will have no effect on growing season length or winter range, and the only mechanism for causing ecosystem change will be the increased AgI and the increased amount of water flowing through the watersheds. Since the soil is saturated in the spring by even low amounts of snowmelt, the increased water will not prolong the plant growing season into an otherwise droughty summer. Of course, snow cover duration is affected by spring air temperatures, which presumably is not affected by cloud seeding.

The augmentation of winter snowpack by cloud seeding with AgI is a technological innovation that may well be appropriate for our civilization. Before making such a program operational, however, we recommend the following:

1. Consider the development of a seeding agent, other than AgI, that would readily break down and never accumulate to toxic concentrations.
2. Conduct a careful analysis of what the additional water will contribute, directly and indirectly, to future salinization problems downstream.
3. Consider the desirability of watershed management alternatives that could provide the same amount of additional water as winter cloud seeding.
4. Encourage, in cooperation with other land management agencies, research to determine the combined ecological effect of all major human influences in certain areas.
5. Plan a monitoring system adequate to detect ecological problems before they become serious.

6. Verify, through appropriate studies, the percentage increase and deposition pattern (elevation, new banks, etc.) of additional snow produced by cloud seeding; and the effect of this additional snow on nutrient leaching, stream hydrographs, and snow cover duration.

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SUMMARY

Using a variety of research approaches, an attempt was made to evaluate the potential effect of winter snowpack augmentation, using silver iodide, on certain key components and processes in several ecosystems in the Medicine Bow Mountains of Wyoming. Financial restrictions did not permit a complete study of the ecosystems and consequently the report is an environmental impact statement for only certain ecosystem characteristics. In addition to baseline data, the report includes the results of eight separate studies:

1. The impact of snow on elk (p. 105).
2. The impact of snow on deer (p. 135).
3. The impact of snow on herbaceous and shrubby vegetation (p. 175).
4. The effect of snow accumulation on litter decomposition and nutrient leaching (p. 215).
5. The relationship between trout ecology and annual snowpack (p. 225).
6. The effect of spring runoff on subalpine lake phytoplankton (p. 259).
7. Silver iodide: its natural concentration, its movement in an alpine ecosystem, and its effect on 2 plant species (p. 329).
8. Silver iodide: acute toxicity, tissue distribution, and subcellular distribution in rainbow trout (p. 353).

The results can be summarized as follows:

1. A large amount of baseline data in the report (pp. 5-104) provides for evaluating the ecological impact of snowpack augmentation using silver iodide when it occurs. This assumes that a monitoring program will be initiated, as we recommend, shortly after the cloud-seeding program begins. If cloud seeding does not begin for 5 to 10 years, then it will be necessary to re-evaluate some of the

baseline data. Changes in ecosystems occur for a variety of reasons.

2. Annual snowfall and streamflow vary over 100 percent. Over 80 percent of the runoff occurs between April and July. Permanent snowbanks exist around Medicine Bow Peak, and many snowbanks above 2700 m persist until mid-July. About 8 percent of the forest understory near Headquarters Park (ca. 3000 m) was still snow covered on July 12, 1974. Continuous snow cover is common in many areas until the end of June. In the fall snow begins to accumulate in late September or during October.

   Air temperature in late spring appears to be more important than snow depth for regulating the date and magnitude of peak flow, as well as the general shape of the hydrograph (pp. 247 - 249).

3. Human utilization of the Mountains is extensive. Being almost entirely within the Medicine Bow National Forest, the area is subject to multiple use which includes recreation, grazing of sheep and cattle, lumbering, wildlife, and water. Although the population density in southeastern Wyoming is low, the area is a major recreation area for the developing megalopolis along the foothills of the Colorado front range. Recreational use is increasing, both in the summer and winter. Many people, including lumbermen and sheepmen, would be concerned if spring access is delayed due to winter cloud seeding. Cattlemen would probably not be concerned, assuming they can be assured that cloud seeding will not cause flooding or snow accumulation below 2700 m; their animals graze and calve at lower elevations.

4. Up to 80 or 90 percent of annual decomposition may occur under snow, despite a temperature of near 0°C. No effect of a prolonged 10-day snow cover duration on litter decomposition rate could be observed with the litter bag technique that we used.

Mineral elements (plant nutrients) released by decomposition and weathering are leached from the soil by snowmelt water, probably in proportion to the amount of water moving through the soil profile. Cloud seeding will increase the amount of water moving through the watersheds, and increased nutrient loss can be expected. We do not know the ecological significance in the Medicine Bow Mountains of 1) increased nutrient loss from the terrestrial ecosystems, or 2) increased nutrient gain to the aquatic ecosystems. Data are presented on the chemical composition of snow, leachate, and stream water.

5. The report describes how snow accumulation does affect plant species composition and plant growth, probably most directly by shortening the growing season but also by providing moisture later into the growing season for plants adjacent to snowbanks. Since cloud seeding may prolong snowbank duration for only 1.5 to 3 days, assuming a 15 percent increase in snow, the most immediate effect will probably be to increase the size of the patches of vegetation that characterize snowbank locations at about 3000 m, where snowbanks now persist until early July. The ecological significance of this effect is probably minor. Year-to-year variations in snowfall provide year-to-year variations in growing season length for some species at higher elevations, and this may be critical to their survival. For example, one long growing season for Vaccinium scoparium could allow sufficient carbon fixation to sustain the plant during several subsequent short growing seasons. Cloud seeding probably will not greatly modify the vegetation unless:

   a) snow duration is prolonged for more than 3 or 4 days longer than is normal on a given site, especially where snow usually lasts until early July;

b) the additional snow is sufficient to modify the existing soil moisture regime;
c) new snowbanks are formed;
d) periodic low snowfall years (long growing season years) no longer occur; or
e) some now unknown, indirect effects result from prolonged snow duration and lead to vegetation change, perhaps, for example, by providing a more favorable habitat for pocket gophers.

Current information suggests that none of the above are very likely to occur, but the data are minimal.

Lists of forest understory species that decrease or increase with longer persisting snow are included. We do not now know of rare or endangered species (plant or animal) that would be driven to extinction by augmented snowfall, though there may be some. The phenology and physiology of several plant species suggest that adaptation to short growing season has been important in their evolution, which in turn suggests that any further shortening of the growing season would not be desirable. Data for Vaccinium scoparium indicate that a growing season of about 100 days is necessary for a positive carbon balance in this species.

6. Many elk and mule deer occur in the area, spending the summer dispersed in the Mountains and wintering as herds in the foothills or adjacent plains below 2700 m. Fall migration may be triggered by snow accumulation. In the spring neither deer nor elk push the snowline as they leave the winter range, but rather remain 1 to 2 km behind where the vegetation is greener. Calving and fawning occur some distance below the retreating snowline. Cloud seeding resulting in only 15 to 20 percent more snow would affect the elk and mule deer adversely only if 1) it is done early in the fall, forcing the animals onto the winter

range earlier than usual; 2) snow depth is increased on the winter range (which is not likely if it is true that snow depth will be increased only above 2700 m); 3) if late spring snows are promoted during or soon after the calving and fawning season (late May to early June); or 4) if snow duration at higher elevations is prolonged more than a few days, thereby causing prolonged use of the winter range (which is unlikely according to research done by the U.S.F.S.).

Elk are better able to tolerate deep snow on the winter range than are mule deer; approximately 88 percent of the mule deer died in the winter of 1972-73, due to both early snows that caused prolonged use of the winter range, and heavy snow accumulation on the winter range which prevented adequate animal nutrition. The deer we observed had a difficult time if snow depth exceeded 0.3 m on the winter range. Wind is a critical factor affecting animal location in the winter. We observed no deer or elk mortality due to unsuccessful crossings of flooded streams.

Sagebrush and other shrubs are important winter food for both deer and elk. Elk usually winter at slightly higher elevations (but still in the foothills) than the deer. If cloud seeding increases snow depths on the elk winter range, then the elk could move further down to the deer winter range, creating excessive competition for food and downgrading the quality of the range vegetation. The deer would suffer most. Current data suggest that this will not happen, but careful monitoring should be done to verify that cloud seeding will not increase snowpack in the foothills below 2600 m. Most deer winter range is considered to be in poor condition at the present time. Current information suggests that cloud seeding will not significantly increase competition between wildlife and domestic livestock.

7. Two hypotheses were tested that relate to effect of cloud seeding on subalpine lake phytoplankton:
   a) During spring the volume flow of runoff is above a "critical" level, flushing losses of the phytoplankton exceed photosynthetic gains, and the algal population decreases.
   b) If the above is true, weather modification will increase the volume flow of runoff, and hence decrease the algal standing crop to levels lower than would otherwise occur.

   Using modeling techniques and data from Libby Lake, we conclude that both hypotheses are correct. However, natural runoff already has such a large impact on lake phytoplankton that an additional 10 to 15 percent in years of less than maximum snowpack will probably not cause significant or undesirable changes. The lakes will not suffer any perturbation that would not occur in the absence of cloud seeding. Phytoplankton biomass is affected also by spring air temperature, epilimnion depth, and wind, which presumably will not be affected by winter cloud seeding. The water retention time (turnover time) in the subalpine lakes is very short, e.g. 7-10 days in Libby Lake.
8. Fish growth is relatively slow in the Medicine Bow Mountains due to cold water, short growing seasons, low nutrient availability, and dense fish populations. Data on fish food habits, population dynamics, biomass, movement, and drift are presented. The time and magnitude of peak stream flow are important in determining the species composition and amount of food available to trout, but additional snow from cloud seeding will probably not modify food availability unless cloud seeding results in higher or colder spring air temperatures. Our data suggest that increased volume flow in streams would lower

spring water temperature and shorten the growing season, which would in turn reduce trout production. The extent to which cloud seeding will modify volume flow should be determined. A 15 percent increase in snowpack probably would not affect trout production greatly. The production of trout and benthic invertebrates apparently are influenced as much by variations in the pattern of runoff and by late summer air temperatures as by the amount of snow and runoff.

Stream invertebrate biomass was not affected significantly by differences in total volume flow during the period of study.

9. The mean silver concentration in the soils, foliage, and litter of the Medicine Bow Mountains is 0.047 ppm, 0.010 ppm, and 0.021 ppm, respectively, with the maximum observed concentration being 0.208 ppm. Silver concentrations for different areas in the Mountains and for different vegetation types are presented beginning on p. 12. Less variation in the Ag data was evident in the fall than in the spring.

Regression analyses suggested that an increase in soil Ag would result in grass and aspen accumulating more Ag than spruce and pine, but the difference is very slight. A one unit increase in soil Ag concentration theoretically would result in a 0.03 unit increase in aspen and grass foliage Ag and a 0.02 unit increase in spruce and pine foliage Ag. Experimental results suggested that grass and forb plants will accumulate 15 to 26 times more Ag when the Ag content of the soil is at some point between 0.12 and 0.24 ppm than when the soil contains 0.12 ppm or less. Increasing the Ag content of the soil from 0.24 to 0.48 ppm causes little additional accumulation. Grasses accumulated significantly more Ag than forbs. Our data suggest that the amount of AgI added to the soil by cloud seeding

will not have adverse effects on lodgepole pine and tufted hairgrass seedlings (and probably other associated plants) until the concentrations are 100 to 1,000 times greater than those naturally found in the soils of the Medicine Bow Mountains. We estimate, on the basis of what we now know, that it would take approximately 450 years for cloud seeding to double the natural Ag concentration in the soils of the Medicine Bow Mountains, except near generators.

Our experiments suggested that most Ag resulting from cloud seeding will remain in the top few cm of soil, but the Ag concentration of runoff water from alpine meadows may increase in direct proportion to the amount of Ag added to the land surface. We do not know whether AgI applied during cloud seeding will move in the same manner as the AgI applied by sprinkling to our study areas.

Runoff and soil erosion, which are considerable in the Medicine Bow Mountains as evidenced by the murky water of spring, could contribute to the Ag content of streams and lakes. (We did not study Ag concentrations in the aquatic ecosystems of the Medicine Bow Mountains.) Once the concentration of Ag in the soil is doubled or tripled, the rate of surface accumulation of Ag could increase due to increased uptake by plants and subsequent deposition on the surface in plant residue. In this way more Ag could become available for surface runoff to either streams or terrestrial depressions.

The report describes experiments which suggest that rainbow trout can tolerate up to 10 g AgI per kg of feed and 1 mg per liter of water. Further research is needed to determine if the reactions of Ag with other compounds in the air and soil will produce either more toxic or less toxic effects. Information on the regional and sub-cellular distribution of Ag is presented.

10. The general discussion emphasizes the need for pilot studies; the need for accurate projections on the amount, distribution and duration of additional snow produced by cloud seeding in order to accurately predict ecological impact; the fact that cloud seeding would be one additional change imposed on other changes already imposed by man; and that there is the potential for indirect, undesirable impacts on areas downstream from where the seeding occurs. A general integration of the results for the Medicine Bow Mountains is presented, and six recommendations are listed that seem desirable from an ecological perspective (p. 370).

APPENDIX I. Common names and authorities of species listed in the text by genus and species only. Nelson (1974)* provides a complete listing of the vascular plants known to occur in the Medicine Bow Mountains.

Scientific Name	Common Name
Abies lasiocarpa (Hook.) Nutt.	Subalpine fir
Achillea lanulosa Nutt. (Achillea millefolium L.)	Western yarrow
Agoseris glauca (Pursh) Raf.	Pale agoseris
Agrogyron trachycaulum (Link) Malte	Slender wheatgrass
A. spicatum (Pursh) Scribn. & Smith	Bluebunch wheatgrass
Agrostis idahoensis Nash	Idaho bent
A. thurberiana Hitchc.	Thurber bent
Amelanchier alnifolia Nutt.	Saskatoon serviceberry
Androsace sp.	Rockjasmine
Angelica grayi Coult. & Rose	Grays angelica
Antennaria rosea Greene	Rose pussytoes
Arenaria obtusiloba (Rydb.) Fernald	Twinflower sandwort
A. rubella (Wahlenb.) J. E. Smith	Sandwort
Arnica cordifolia Hook.	Heartleaf arnica
A. latifolia Bong.	Orange arnica
A. mollis Hook.	Hairy arnica
Artemisia frigida Willd.	Fringed sagewort
A. scopulorum Gray	Alpine sagewort
A. tridentata Nutt.	Big sagebrush
Aster alpigenus (T. & G.) A. Gray	Aster
Astragalus miser Dougl. ex Hook.	Weedy milkvetch
Balsamorhiza sagittata (Pursh) Nutt.	Arrowleaf balsamroot
Calamagrostis purpurascens R. Br.	Purple reedgrass
C. rubescens Buckl.	Pine reedgrass
Caltha leptosepala DC.	Elkslip marshmarigold
Campanula rotundifolia L.	Bluebell bellflower

* Nelson, B. E. 1974. Vascular plants of the Medicine Bow Mountains, Wyoming. M.S. Thesis, Department of Botany, University of Wyoming.

APPENDIX I. (Cont'd)

Scientific Name	Common Name
Carex albo-nigra Mack.	Blackandwhitescaled sedge
C. aquatillis Wohl.	Water sedge
C. ebenea Rydb.	Ebony sedge
C. geyeri Boott	Elk sedge
C. illota Bailey	Sheep sedge
C. rossii Boott	Ross sedge
Ceanothus sp.	Ceanothus
Cerastium arvense L.	Starry cerastium
Chimaphila umbellata (L.) Bart.	Princespine pipsissewa
Chrysopsis villosa (Pursh) Nutt. (Heterotheca villosa (Pursh) Shinners)	Narrowleaf goldenaster
Chrysothamnus sp.	Rabbitbrush
C. nauseosus (Pall.) Britt.	Rubber rabbitbrush
C. viscidiflorus (Hook.) Nutt.	Douglas rabbitbrush
Claytonia lanceolata Pursh	Lanceleaf Springbeauty
Danthonia intermedia Vasey	Oatgrass
Delphinium nelsonii Greene	Nelson larkspur
Deschampsia caespitosa (L.) Beauv.	Tufted hairgrass
Draba aurea Vahl	Golden draba
D. stenoloba Ledeb.	Alaska draba
Eleocharis pauciflora (Lighf.) Link	Fewflowered spikerush
Epilobium alpinum L.	Alpine willowherb
E. angustifolium L.	Fireweed willowherb
E. halleanum Hausskn.	Willowherb
E. hornemanni Reichenb.	Horneman willowherb
Erigeron compositus Pursh	Fernleaf fleabane
E. peregrinus (Pursh) Greene	Peregrine fleabane
E. simplex Greene	Oneflower fleabane
Eriogonum umbellatum Torr.	Sulfur wildbuckwheat
Erythronium grandiflorum Pursh	Lambstongue troutlily

APPENDIX I. (Cont'd)

Scientific Name	Common Name
Festuca brachyphylla Schult.	Fescue
F. idahoensis Elmer	Idaho fescue
F. rubra L.	Red fescue
Gentiana algida Pall.	Gentian
G. barbellatus Engelm.	Gentian
Geum rossii (R. Br.) Ser.	Alpine avens
Hesperochloa kingii (see Leucopoa)	King spikefescue
Hieracium albiflorum Hook.	White hawkweed
H. gracile Hook.	Slender hawkweed
Hordeum brachyantherum Nevski	Meadow barley
Juncus drummondii E. Mey.	Drummond rush
J. mertensianus Bong.	Mertens rush
Juniperus communis L.	Common juniper
J. scopularum Sarg.	Rockymountain juniper
Koelaria cristata (L.) Pers.	Prairie Junegrass
Leucopoa kingii (S. Wats.) W. A. Weber (Hesperochloa kingii (Wats.) Rydb.)	King spikefescue
Lewisia pygmaea (Gray) Robins.	Least lewisia
Ligusticum porteri Coult. & Rose	Porters lovage
Lupinus argenteus Pursh	Silvery lupine
Luzula spicata (L.) DC.	Spike woodrush
Mahonia repens (Lindl.) G. Don (Berberis repens Lindl.)	Oregon grape, Creeping barberry
Mertensia alpina (Torr.) G. Don	Alpine bluebells
M. viridis A. Nels.	Greenleaf bluebells
Mimulus lewisii Pursh	Lewis monkeyflower
Opuntia polyacantha Haw.	Plains pricklypear
Pedicularis groenlandica Retz.	Elephanthead lousewort
P. parryi Gray	Parry lousewort
P. racemosa Dougl. ex Hook.	Lousewort
Phleum alpinum L.	Alpine timothy

APPENDIX I. (Cont'd)

Scientific Name	Common Name
Phlox multiflora A. Nels.	Phlox
Picea engelmannii Parry ex Engelm.	Engelmann spruce
Pinus contorta Dougl. ex Loud.	Lodgepole pine
Plantago tweedii Gray	Tweedy plantain
Poa alpina L.	Alpine bluegrass
P. annua L.	Annual bluegrass
P. cusickii Vasey	Cusick bluegrass
P. nervosa (Hook.) Vasey	Wheeler bluegrass
P. pattersonii Vasey	Patterson bluegrass
P. reflexa Vasey & Scribn.	Nodding bluegrass
P. rupicola Nash	Timberline bluegrass
Polemonium viscosum Nutt.	Sticky polemonium
Polygonum bistortoides Pursh	American bistort, knotweed
Polytrichum juniperinum	Juniper haircapgrass, a moss
Potentilla diversifolia Lehm.	Blueleaf cinquefoil
Potentilla spp.	Cinquefoil
Purshia tridentata (Pursh) DC.	Antelope bitterbrush
Pyrola secunda L.	Sidebells pyrola
Ranunculus alismaefolius Geyer ex Benth.	Plantainleaf buttercup
R. eschscholtzii Schlect.	Buttercup
Rorippa curvipes Greene (R. obtusa (Nutt.) Britt.)	Spreadingyellow watercress
Rosa woodsii Lindl.	Woods rose
Saxifraga rhomboidea Greene	Diamondleaf saxifraga
Sedum lanceolatum Torr.	Stonecrop
S. rhodanthum Gray	Rosecrown stonecrop
Selaginella densa Rydb.	Spikemoss selaginella
Senecio dimorphophyllus Greene	Groundsel
S. fremontii Torr. & Gray	Fremont groundsel
Shepherdia canadensis (L.) Nutt.	Russett buffaloberry
Sibbaldia procumbens L.	Sibbaldia
Silene acaulis L.	Moss silene

APPENDIX I. (Cont'd)

Scientific Name	Common Name
Solidago spathulata DC.	Coast goldenrod
Spergularia rubra (L.) J. & C. Presel	Sandspurry
Stellaria borealis Bigelow (Stellaria calycantha (Ledeb.) Bong.)	Northern starwort
Stipa columbiana Macoun	Subalpine needlegrass
S. comata Trin. & Rupr.	Needleandthread
S. lettermanii Vasey	Letterman needlegrass
Taraxacum officinale Weber	Common dandelion
Thlaspi alpestre L. (T. montanum L.)	Alpine pennycress
T. glaucum A. Nels. (T. montanum A. Nels.)	Blue pennycress
Trifolium nanum Torr.	Dwarf clover
T. parryi Gray	Parry clover
Trisetum spicatum (L.) Richt.	Spike trisetum
T. woolfii Vasey	Wolfs trisetum
Trollius laxus Salisb.	Globeflower
Vaccinium myrtillus L.	Myrtle whortleberry
V. scoparium Leiberg	Grouse whortleberry, huckleberry
Veronica wormskjoldii Roem. & Schult.	Veronica
Viola adunca Smith	Hookedspur violet
Zigadenus elegans Pursh	Death camas

APPENDIX II. Index of four-letter abbreviations for plant names used in Appendix III.

FORBS AND SHRUBS

ACLA	*Achillea lanulosa* Nutt.
AGGL	*Agoseris glauca* (Pursh) D. Dietr.
ANGR	*Angelica grayi* Coult. & Rose
ANRO	*Antennaria rosea* (D. C. Eat.) Greene
AROB	*Arenaria obtusiloba* (Rydb.) Fern.
ARLA	*Arnica latifolia* Bong.
ARSC	*Artemisia scopulorum* A. Gray
ASAL	*Aster alpigenus* (T. & G.) A. Gray
CARO	*Campanula rotundifolia* L.
CEAR	*Cerastium arvense* L.
DENE	*Delphinium nelsonii* Greene
DRAU	*Draba aurea* M. Vahl
EPAL	*Epilobium alpinum* L.
ERCO	*Erigeron compositus* Pursh
ERSI	*Erigeron simplex* Greene
ERGR	*Erythronium grandiflorum* Pursh
GEAL	*Gentiana algida* Pall.
GEBA	*Gentiana barbellata* Engelm.
GERO	*Geum rossii* (R. Br.) Ser.
LEPY	*Lewisia pygmaea* (A. Gray) Robins.
MEAL	*Mertensia alpina* (Torr.) G. Don
MILE	*Mimulus lewisii* Pursh
PEGR	*Pedicularis groenlandica* Retz.
PEPA	*Pedicularis parryi* A. Gray
PHMU	*Phlox multiflora* A. Nels.
POVI	*Polemonium viscosum* Nutt.
POBI	*Polygonum bistortoides* Pursh
PODI	*Potentilla diversifolia* Lehm.
POSP	*Potentilla* spp.
SARH	*Saxifraga rhomboidea* Greene
SELA	*Sedum lanceolatum* Torr.
SEFR	*Senecio fremontii* T. & G.

SIPR	Sibbaldia procumbens L.
SIAC	Silene acualis L.
SOSP	Solidago spp.
TAOF	Taraxacum officinale L.
THAL	Thlaspi alpestre L.
TRNA	Trifolium nanum Torr.
TRPA	Trifolium parryi A. Gray
UNFB	Unidentified forb taxa
VASC	Vaccinium scoparium Leiberg
VIAD	Viola adunca J. E. Smith

CRYPTOGAMS

SEDE	Selaginella densa Rydb.
UNCM	Unidentified taxa

GRASSES

AGSC	Agropyron scribneri Vasey
AGID	Agrostis idahoensis Nash
DAIN	Danthonia intermedia Vasey
DECA	Deschampsia caespitosa (L.) Beauv.
FEBR	Festuca brachyphylla Schultes
FERU	Festuca rubra L.
KOCR	Koelaria cristata (L.) Pers.
PHAL	Phleum alpinum L.
POAL	Poa alpina L.
POCU	Poa cusickii Vasey
POPA	Poa pattersonii Vasey
PORU	Poa rupicola Nash
STCO	Stipa columbiana Macoun.
STLE	Stipa lettermanii Vasey
TRSP	Trisetum spicatum (L.) Richt.
UNGR	Unidentified grass taxa

WOODRUSH

LUSP	Luzula spicata (L.) DC.

APPENDIX III. Biomass (g/m^2) of live vegetation by taxon in 1972 and 1973 at the Libby Flats, Lake Marie, and Fourlog Park study areas. See p. 24 and p. 25 for study area locations. See Appendix II for a key to the species abbreviations, which are the first 2 letters of the genus name and first 2 letters of the species name. The sampling date is indicated across the top of each table. See p. 60 for discussion.

LIBBY FLATS - 1972

6/26		7/10		7/24		8/07		8/21	
Taxa	g/m^2	Taxa	g/m^2	Taxa	g/m^2	Taxa	g/m^2	Taxa	g/m^2
GERO	47.1	GERO	40.0	GERO	27.6	GERO	30.7	GERO	27.9
ARSC	10.5	ARSC	12.8	POBI	7.0	SEDE	13.3	SEDE	14.8
TRPA	8.7	SEDE	8.1	ARSC	6.4	ARSC	10.9	ARSC	8.6
SEDE	8.3	DECA	7.2	DECA	6.3	DECA	7.7	DECA	4.9
POBI	5.1	TRPA	6.0	TRPA	5.8	TRPA	6.4	TRPA	4.6
AROB	4.7	POBI	4.3	ACLA	3.5	DAIN	5.1	AGSC	4.3
DECA	4.0	CEAR	2.8	AROB	3.1	AROB	3.2	AGID	4.0
PODI	3.4	AGID	2.1	PODI	2.4	CEAR	2.7	AROB	3.9
AGID	2.5	PODI	1.7	CEAR	1.3	ACLA	2.3	PODI	3.4
ACLA	2.5	ACLA	1.5	POSP	1.3	CAAL	2.2	CEAR	2.5
CAEL	1.9	AROB	1.5	AGID	1.2	POBI	1.7	FEBR	2.3
ERSI	1.5	ERSI	1.4	SEDE	1.0	PODI	1.3	ACLA	1.8
CAOB	1.3	POSP	1.1	CAEB	1.0	FEBR	0.9	POBI	1.6
POAL	1.1	ASAL	0.7	ERSI	1.0	AGID	0.9	CAEB	1.5
POVI	1.1	CAEB	0.5	CAEL	0.9	POAL	0.7	MEAL	1.5
SELA	1.0	POAL	0.4	CAAL	0.6	FERU	0.6	POPA	0.7
POSP	0.9	TRSP	0.4	CAOB	0.6	CAOB	0.6	DAIN	0.6
DRAU	0.9	CAOB	0.2	PEPA	0.5	SEFR	0.5	CAOB	0.6
LUSP	0.8	LUSP	0.2	POUI	0.4	ERSI	0.5	SEFR	0.6
SARH	0.3	CAAL	0.2	SEFR	0.4	AGGL	0.4	PEPA	0.6
CAEB	0.3	LEPY	0.2	DAIN	0.3	PEPA	0.4	POAL	0.4
CAAL	0.2	ANGR	0.2	MILE	0.2	ARLA	0.4	THAL	0.3
FEBR	0.2	THAL	0.1	LUSP	0.2	UNCM	0.4	CAAL	0.2
CEAR	0.2	POVI	0.1	UNCX	0.2	KOCR	0.3	ERSI	0.2
LEPY	0.1	PEPA	T	AGGL	0.1	CAEB	0.3	SOSP	0.1
MEAL	0.1	SELA	T	SELA	T	CAEL	0.2	POVI	0.1
ANRO	0.1	GEAL	T	FEBR	T	PEGR	0.2	POSP	0.1
THAL	T	SARH	T	POAL	T	LUSP	0.1	PEGR	T
TAOF	T	KOCR	T	ANRO	T	POVI	0.1	CAEL	T
KOCR	T	MEAL	T	GEAL	T	TRSP	T	KOCR	T
AGGL	T	AGGL	T	Total	75.6	MILE	T	DRAU	T
PEPA	T	ANRO	T			Total	95.0	LUSP	T
Total	108.9	CAEL	T					SELA	T
		MILE	T					ANRO	T
		Total	93.8					UNCX	T
								FERU	T
								TAOF	T
								MILE	T
								Total	92.1

APPENDIX III (Cont'd.) LIBBY FLATS - 1973

6/20		7/04		7/18		8/01		8/15		8/29	
Taxa	g/m^2	Taxa	g/m^2	Taxa	g/m^2	Taxa	g/m^2	Taxa	g/m^2	Taxa	g/m^2
GERO	35.7	GERO	56.6	GERO	59.1	GERO	48.2	GERO	30.9	GERO	11.2
ARSC	10.0	POBI	20.3	ARSC	19.8	ARSC	20.6	ARSC	10.9	ARSC	5.8
DECA	4.8	ARSC	18.5	TRPA	16.4	TRPA	16.4	TRPA	10.6	TRPA	4.3
TRPA	3.5	PHMU	16.2	CEAR	12.5	AROB	8.7	DECA	7.4	DECA	4.0
SEDE	2.7	DECA	10.0	SIAC	11.7	DECA	6.2	CEAR	6.5	DAIN	3.1
PODI	2.0	SEDE	9.5	AROB	6.5	SEDE	5.1	AROB	4.1	CEAR	2.2
AGID	1.8	TRPA	8.1	POBI	6.3	POBI	4.9	CAEB	3.8	FEBR	1.8
CEAR	1.8	PODI	6.0	DECA	5.3	POAL	4.7	DAIN	2.9	AROB	1.8
POAL	1.6	ERSI	5.2	SEDE	4.1	CEAR	3.8	SEDE	2.8	GEBA	1.3
POBI	1.2	ACLA	4.1	DAIN	3.3	ERSI	2.8	ACLA	2.6	CAOB	1.0
AROB	0.9	POAL	3.8	PODI	2.6	ACLA	2.7	PODI	2.5	ACLA	0.9
ACLA	0.8	CEAR	3.4	ACLA	2.4	PODI	2.6	SOSP	2.0	PODI	0.7
PEPA	0.7	AGID	3.1	AGID	2.2	FERU	1.7	AGID	1.8	SEFR	0.7
CAEL	0.6	AROB	2.3	CAEB	1.8	POPA	1.4	SIAC	1.7	PEPA	0.6
SARH	0.6	CAAL	1.8	POPA	1.7	CAEB	1.4	CAOB	1.2	SEDE	0.5
DAIN	0.6	DAIN	1.8	SOSP	1.4	SOSP	1.3	POBI	0.9	AGID	0.5
CAEB	0.5	MEAL	1.7	ERSI	1.1	POSP	1.3	ERSI	0.8	POPA	0.5
UNCM	0.5	THAL	1.6	MEAL	0.9	CAOB	1.2	PEPA	0.8	ERSI	0.5
ERSI	0.4	POPA	1.3	THAL	0.8	AGID	1.1	CAAL	0.7	POBI	0.3
MEAL	0.4	SARH	1.1	CAOB	0.3	SEST	1.1	POVI	0.5	ANRO	0.3
PORU	0.4	POVI	0.6	LUSP	0.3	UNCM	0.6	POPA	0.3	THAL	0.2
THAL	0.3	CAEB	0.6	POAL	0.3	CAEL	0.5	LUSP	0.3	POVI	0.2
POPA	0.3	CAEL	0.6	POVI	0.3	THAL	0.3	THAL	0.3	CAEL	0.2
LUSP	0.2	LUSP	0.4	SEFR	0.3	LUSP	0.2	MEAL	0.3	POAL	0.1
ANRO	0.2	SIAC	0.4	SELA	0.2	PEPA	0.2	FERU	0.2	SELA	0.1
MILE	0.2	PEPA	0.3	CAAL	0.1	AGGL	0.2	FEBR	0.1	AGGL	0.1
LEPY	0.1	SELA	0.3	SARH	0.1	REBR	0.2	POAL	0.1	FERU	0.1
SELA	0.1	FERU	0.3	PEPA	0.1	POVI	0.2	AGGL	0.1	TRSP	T
CAOB	T	PORU	0.2	FEBR	0.1	SIAC	T	DRAU	0.1	CAEB	T
KOCR	T	ANRO	T	LEPY	0.1	MEAL	T	TRSP	0.1	MEAL	T
POVI	T	GEAL	T	CAEL	0.1	CAAL	T	SELA	0.1	PHMU	T
SIAC	T	PEGR	T	ANRO	0.1	SARH	T	GEBA	T	LUSP	T
FEBR	T	AGGL	T	AGGL	T	LEPY	T	SARH	T	CARO	T
GEAL	T	KOCR	T	FERU	T	ANRO	T	ANRO	T	SARH	T
POSP	T	LEPY	T	GEBA	T	TRSP	T	CAEL	T	Total	43.0
Total	72.9	FEBR	T	MILE	T	GEAL	T	Total	97.3		
		Total	180.1	GEAL	T	Total	139.7				
				Total	162.6						

APPENDIX III (Cont'd.) LAKE MARIE - 1972

6/27		7/11		7/25		8/16		8/22	
Taxa	g/m^2	Taxa	g/m^2	Taxa	g/m^2	Taxa	g/m^2	Taxa	g/m^2
GERO	28.7	GERO	35.9	GERO	38.9	GERO	58.2	GERO	77.7
ARSC	5.6	ARSC	7.7	CAAL	10.5	SEDE	10.6	ARSC	11.9
AROB	2.7	DECA	5.1	ARSC	8.6	ARSC	9.0	DECA	10.1
DECA	2.6	CAAL	3.7	ERSI	3.9	DECA	5.8	UNCM	8.6
POBI	2.4	POBI	3.2	DECA	3.8	UNCM	4.1	AGID	7.1
SIPR	2.4	SIPR	2.9	POBI	2.0	SIPR	3.6	SEDE	6.6
ANGR	2.3	ERSI	2.7	PODI	1.8	ERSI	3.3	ERSI	6.2
ERSI	1.9	TRPA	1.9	AROB	1.3	CAEB	3.2	AROB	4.2
PODI	1.4	SEDE	1.4	TRPA	1.2	AROB	2.3	PODI	2.5
SEDE	1.2	GEAL	1.3	SIPR	1.2	POAL	2.1	TRPA	2.2
CAAL	0.9	AROB	1.3	SEDE	0.7	PODI	1.8	SIPR	1.9
AGID	0.7	UNCM	1.1	AGID	0.6	POBI	1.4	GEAL	1.9
TRPA	0.5	PODI	0.8	ANGR	0.6	TRPA	1.4	POBI	1.2
ERCO	0.5	AGID	0.7	PEPA	0.5	AGID	0.7	CAEB	0.7
CAEL	0.3	ERCO	0.6	GEAL	0.5	PEGR	0.6	CAAL	0.3
THAL	0.3	THAL	0.4	CAEL	0.4	FEBR	0.4	CEAR	0.1
PEGR	0.3	GEBA	0.3	TRNA	0.4	CAEL	0.3	THAL	0.1
SARH	0.1	CEAR	0.2	THAL	0.3	DAIN	0.3	PEPA	0.1
CAOB	0.1	CAOB	0.1	PEGR	0.2	CAOB	0.2	CAOB	T
POSP	0.1	CAEB	0.1	SIAC	0.2	CEAR	0.2	PEGR	T
PEPA	0.1	PEGR	T	LUSP	T	PEPA	0.2	TRSP	T
TRSP	T	SARH	T	TRSP	T	GEAL	0.1	LUSP	T
ACLA	T	SIAC	T	LEPY	T	TRSP	0.1	AGGL	T
KOCR	T	LEPY	T	CAOB	T	LEPY	0.1	FEBR	T
POAL	T	LUSP	T	CEAR	T	ACLA	T	Total	143.5
SIAC	T	TRSP	T	SELA	T	LUSP	T		
Total	55.3	Total	71.6	Total	77.4	THAL	T		
						Total	109.9		

APPENDIX III (Cont'd.) LAKE MARIE - 1973

7/05		7/19		8/02		8/16		8/30	
Taxa	g/m^2	Taxa	g/m^2	Taxa	g/m^2	Taxa	g/m^2	Taxa	g/m^2
GERO	31.9	GERO	49.2	GERO	66.2	GERO	37.7	GERO	32.7
ARSE	9.3	ARSC	12.8	ARSC	9.6	ARSC	8.1	DECA	7.3
UNCM	7.4	SEDE	5.2	SEDE	9.2	DECA	7.2	ERSI	5.5
DECA	2.9	ERSI	5.0	DECA	7.3	ERSI	4.0	ARSC	5.2
SIAC	2.0	DECA	3.7	ERSI	6.3	CAEB	3.5	SIPR	2.8
ERSI	1.2	SIPR	3.4	PODI	4.2	POBI	2.7	PODI	2.6
AROB	1.2	UNCM	2.5	POBI	3.1	SIPR	2.4	GEAL	2.6
AGID	1.0	POBI	2.2	TRPA	2.2	PODI	1.9	TRPA	1.4
POBI	0.7	AGID	1.6	SIPR	2.1	TRPA	1.7	POBI	1.2
CEAR	0.7	TRPA	1.5	AROB	1.4	GEBA	1.1	CAEB	1.0
LEPY	0.7	LEPY	1.4	CAEB	1.1	CAAL	0.7	AROB	0.9
CAAL	0.6	PODI	1.2	PEGR	0.9	AGID	0.7	ANGR	0.8
PODI	0.5	CAEB	1.1	AGID	0.6	AROB	0.2	THAL	0.8
SEDE	0.4	AROB	1.1	PEPA	0.2	PEGR	0.2	AGID	0.6
CAOB	0.4	THAL	1.1	TRSP	0.1	PEPA	0.2	PEPA	0.4
TRPA	0.1	ASAL	1.0	LEPY	0.1	GEAL	0.1	CAAL	0.3
THAL	0.1	CAOB	0.7	CEAR	0.1	THAL	0.1	UNCM	0.3
CAEL	0.1	LUSP	0.6	GEAL	T	SEDE	T	FERU	0.3
POAL	0.1	CAEL	0.5	SARH	T	CAOB	T	PEGR	0.3
MILE	T	MILE	0.4	CAAL	T	LUSP	T	LUSP	0.2
POPA	T	PEGR	0.3	LUSP	T	SARH	T	CEAR	0.2
GEAL	T	FEBR	0.2	THAL	T	CAEL	T	LEPY	0.1
SARH	T	KOCR	0.2	ASAL	T	LEPY	T	SEDE	T
CAEB	T	PEPA	0.1	CAEL	T	FERU	T	TRSP	T
PEPA	T	SARH	T	Total	114.8	TRSP	T	POPA	T
LUSP	T	GEAL	T			Total	72.5	SOSP	T
TRSP	T	TRSP	T					CAEL	T
FERU	T	UNCX	T					MILE	T
FEBR	T	POAL	T					PORU	T
PEGR	T	POSP	T					Total	67.4
PORU	T	SIAC	T						
Total	61.2	Total	97.3						

APPENDIX III (Cont'd.) FOURLOG PARK - 1972

7/12		7/26		8/09		8/23	
Taxa	g/m^2	Taxa	g/m^2	Taxa	g/m^2	Taxa	g/m^2
CAEB	20.9	CAEB	16.0	CAEB	18.4	CAEB	19.0
PODI	8.4	STLE	11.1	STCO	12.7	PODI	11.0
DECA	8.2	PODI	7.9	PODI	6.8	STCO	7.9
STLE	3.2	ERSI	5.9	ACLA	6.4	ERSI	7.3
POCU	2.9	ACLA	5.2	ERSI	4.3	PORU	6.8
PHAL	1.9	SIPR	4.8	POSP	4.2	ACLA	4.7
ACLA	1.8	PHAL	4.4	PHAL	3.6	STLE	4.1
SIPR	1.4	AGGL	3.1	TAOF	3.4	AGGL	2.0
TAOF	1.3	POSP	3.0	POCU	2.9	DECA	1.8
AGGL	1.2	TAOF	2.5	AGGL	1.7	PHAL	1.5
STCO	1.1	POCU	2.5	STLE	1.3	DAIN	1.5
LEPY	0.8	DECA	2.3	DECA	0.6	SIPR	1.2
ERSI	0.7	SEFR	1.0	SIPR	0.5	ASAL	1.0
UNCX	0.4	MILE	0.3	ASAL	0.5	POCU	0.7
DRAU	0.3	POBI	0.3	THAL	0.3	AROB	0.6
ERGR	0.2	CEAR	0.1	GEAL	T	TAOF	0.4
POBI	0.1	DAIN	0.1	POBI	T	POAL	0.4
MILE	0.1	UNCM	0.1	SEFR	T	UNCM	0.4
ARLA	0.1	LEPY	T	TRSP	T	MILE	0.3
TRSP	0.1	AROB	T	LUSP	T	KOCR	0.3
DAIN	0.1	PEPA	T	Total	67.7	CAOB	0.2
ASAL	T	Total	70.6			POBI	0.2
POSP	T					ANRO	0.1
AROB	T					UNGR	0.1
THAL	T					POSP	0.1
Total	55.2					TRPA	T
						CEAR	T
						ARLA	T
						UNCX	T
						LUSP	T
						THAL	T
						TRSP	T
						Total	73.5

APPENDIX III (Cont'd.) FOURLOG PARK - 1973

7/06		7/20		8/03		8/17		8/31	
Taxa	g/m^2	Taxa	g/m^2	Taxa	g/m^2	Taxa	g/m^2	Taxa	g/m^2
CAEB	13.7	LEPY	28.7	CAEB	20.5	CAEB	20.5	CAEB	24.3
PODI	12.4	POCU	27.9	SIPR	18.7	STLE	17.1	STLE	16.0
ERSI	12.1	CAEB	23.7	PODI	17.8	PODI	13.8	PODI	8.9
STCO	7.1	PODI	11.6	STLE	14.1	ERSI	9.1	STCO	6.9
STLE	4.9	ERSI	8.2	ERSI	13.8	STCO	7.5	SIPR	5.3
LEPY	3.6	STLE	7.9	POCU	11.1	ACLA	6.9	ACLA	4.6
PHAL	3.2	DECA	6.4	ACLA	6.1	PHAL	6.4	PORU	4.2
AGGL	2.6	PHAL	6.1	PHAL	4.6	PORU	6.3	DAIN	4.0
POCU	2.5	ACLA	4.6	TAOF	3.7	AGGL	5.2	ERSI	3.8
SARH	2.4	AGGL	4.1	AGGL	3.5	TAOF	4.4	POCU	3.3
SIPR	1.8	SIPR	3.5	STCO	3.2	CAAL	3.4	AGGL	2.4
ACLA	1.5	STCO	2.9	PORU	2.1	DECA	3.1	SOSP	1.6
DECA	0.9	UNCM	2.5	LEPY	2.0	SIPR	2.4	PHAL	1.4
POAL	0.6	TAOF	1.9	TRSP	1.1	POCU	1.5	TAOF	1.2
AGID	0.5	POAL	1.3	POAL	1.0	MEAL	0.9	UNCX	0.8
ASAL	0.4	ARLA	0.7	AROB	0.9	LEPY	0.7	SEFR	0.3
ERGR	0.3	MILE	0.6	DECA	0.5	POAL	0.7	EPAL	0.2
PORU	0.3	POBI	0.5	SEFR	0.3	POSP	0.5	AROB	0.1
TAOF	0.2	PORU	0.3	POBI	0.3	SOSP	0.4	MILE	0.1
POBI	0.2	AROB	0.3	UNCM	0.3	AROB	0.3	POBI	T
UNCM	0.2	DAIN	0.3	THAL	0.2	POBI	0.3	TRSP	T
POSP	0.2	UNCX	0.2	ERGR	T	TRSP	0.2	CEAR	T
ANRO	0.2	ANRO	0.1	ANRO	T	MILE	0.1	THAL	T
THAL	0.1	ERGR	0.1	SEDE	T	CARO	T	DAIN	T
AROB	0.1	LUSP	0.1	SOSP	T	ASAL	T	Total	88.6
MILE	T	TRPA	T	UNCX	T	VIAD	T		
ARLA	T	DENE	T	Total	126.0	THAL	T		
CEAR	T	SARH	T			ARSC	T		
Total	72.9	THAL	T			DAIN	T		
		VIAD	T			SEFR	T		
		Total	144.8			VASC	T		
						Total	111.8		